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Rebalancing River Lateral Connectivity: An Interdisciplinary Focus for Research and Management

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ABSTRACT

Lateral connectivity between rivers and terrestrial landscapes is critical for both river and landscape health. Due to widespread anthropogenic degradation of riverscapes, river management is aiming to connect rivers to floodplains, riparian zones, and wetlands, putting a spotlight on lateral connectivity. However, there is currently no consensus on how to conceptualize and study lateral connectivity in rivers across disciplines. Here, we review lateral connectivity between riverscapes and terrestrial landscapes. We focus on the natural sciences, considering hydrology, geomorphology, ecology and biogeochemistry, but also consider social connectivity and the management and restoration of lateral connectivity. We emphasize the importance of considering the bidirectional nature of lateral connectivity, operating both into and out of river channels and the balance between these directions. The resulting "lateral connectivity balance" provides a framework to understand natural spatial and temporal variability in connectivity. Anthropogenic impacts have swung the balance of lateral connectivity, enhancing the transport of materials into and through river networks while suppressing fluxes from rivers to adjacent landscapes. We conclude that further research at the interfaces between the aquatic and terrestrial components of riverscapes is critical to advance our conceptual understanding of river and catchment systems. We propose that such research should be framed within the paradigm of "rebalancing" lateral connectivity, explicitly recognizing the natural bidirectionality of laterally connecting processes, the significance of the hydrologic, geomorphic, and biologic functions they support, and the value to society of the ecosystem services and climate change resilience they provide.

1 | Introduction

Rivers connect landscapes by providing pathways for the movement of water, sediments, solutes, and biota. Connectivity and disconnectivity have been fundamental concepts in the development of river science across many disciplines including hydrology (e.g., Ali and Roy 2009; Bracken et al. 2013; Rinderer, Ali, and Larsen 2018), geomorphology (e.g., Wohl et al. 2019; Poeppl, Polvi, and Turnbull 2023), ecology (e.g., Amoros and Roux 1988; Fuller and Death 2018; Liczner et al. 2024), biogeochemistry (e.g., T. Covino 2017), and sociology (e.g., Kondolf and Pinto 2017; Dunham et al. 2018). Thus, the concept of connectivity has shaped the way we conceptualize, research, manage, and restore rivers (Bracken et al. 2013; Parsons et al. 2015; Keesstra et al. 2018; Rinderer, Ali, and Larsen 2018; Wohl et al. 2019; Allen et al. 2020).

Connectivity is referenced to three orthogonal axes: longitudinal, vertical, and lateral to the course of the river, and varies through both space and time (Ward 1989). Lateral connectivity, the focus here, describes the bidirectional flux of materials, energy, and organisms between waterscapes (here defined by the current extent of inundated surface water bodies, including river channels, ponds, wetlands, and flooded habitats), and adjacent landscapes (here defined as terrestrial features and habitats, including dry valley floors, valley sides, terraces, and hillslopes). Lateral connectivity is bidirectional (Figure 1). Materials, organisms, and energy move from landscapes (L) *into* waterscapes (W) (landscape ➔ waterscape, denoted by L ➔ W in this manuscript), for example, via tributary inflow, subsurface transport, overland runoff, and anthropogenic drainage. In contrast, fluxes also occur in the other direction: *out of* waterscapes and *into* the surrounding landscape (waterscape ➔ landscape; W ➔ L). For example, overbank flood events drive W ➔ L fluxes, as they deposit water, sediments, and organisms on the floodplain, while some animals may move actively between the waterscape and landscape irrespective of flow stage.

The boundaries between waterscapes and landscapes are not fixed, but vary through time (e.g., Stanley, Fisher, and Grimm 1997). These lateral expansions and contractions drive many connecting processes (Junk, Bayley, and Sparks 1989) and support transitional habitats, which switch between aquatic and terrestrial. Both L ➔ W and W ➔ L fluxes involve a wide range of materials, energy, and organisms (and therefore scientific disciplines) including not only water, but sediments, solutes, biota, and people. Consequently, bidirectional lateral connectivity is integral to, and essential for, the health of rivers and landscapes, and the provision of many riverine ecosystem services (Leigh and Sheldon 2009; Desjonquères et al. 2018; Petsch et al. 2023; Figure 1).

Modifications to lateral connectivity represent some of the most pervasive human impacts on river systems (Figure 2). Across most of the planet, river management has been undertaken with the specific intention of reducing W ➔ L fluxes of water, sediment, and energy, for example, by enlarging the channel and raising artificial levees. Simultaneously, humans have increased the rate of fluxes of material L ➔ W, for example, through land drainage (Blann et al. 2009; Gramlich et al. 2018; Gurnell and Downs 2021; Morrison et al. 2023). In parallel, catchment-scale deforestation, urbanization, and water resource development have indirectly reinforced these modifications to lateral connectivity through their effects on river flow and sediment regimes (Simon and Rinaldi 2006; Walter and Merritts 2008). In combination, the intended and unintended consequences of anthropogenically driven changes to river systems have typically exaggerated L ➔ W connectivity while suppressing fluxes of material W ➔ L. The pervasive extent of reductions in W ➔ L lateral connectivity are largely responsible for the global decline in transitional habitats: riparian zones, wetlands and floodplains, and the ecosystem services these provide (Jones et al. 2010; Schneider et al. 2017; Rajib et al. 2023; Morrison et al. 2023). Similarly,

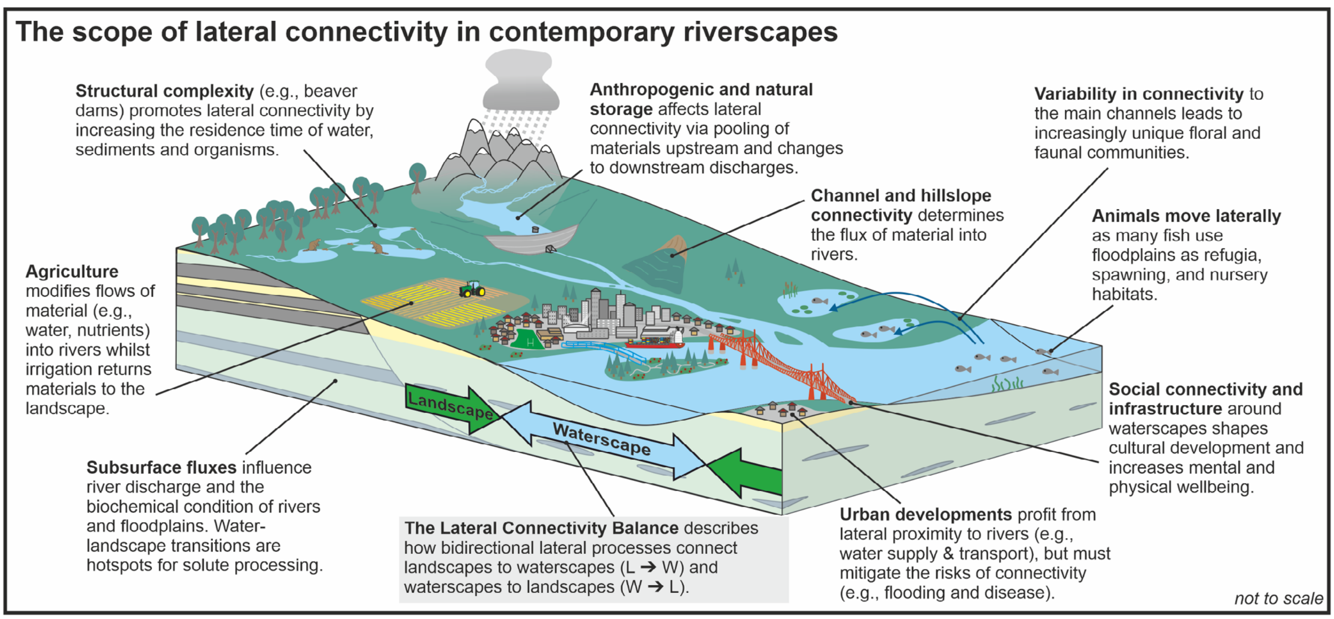

FIGURE 1 | Examples of lateral connectivity in a human-modified riverscape. The lateral connectivity balance describes the relative importance of fluxes of material into waterscapes from landscapes (L ➔ W) and vice versa (W ➔ L).

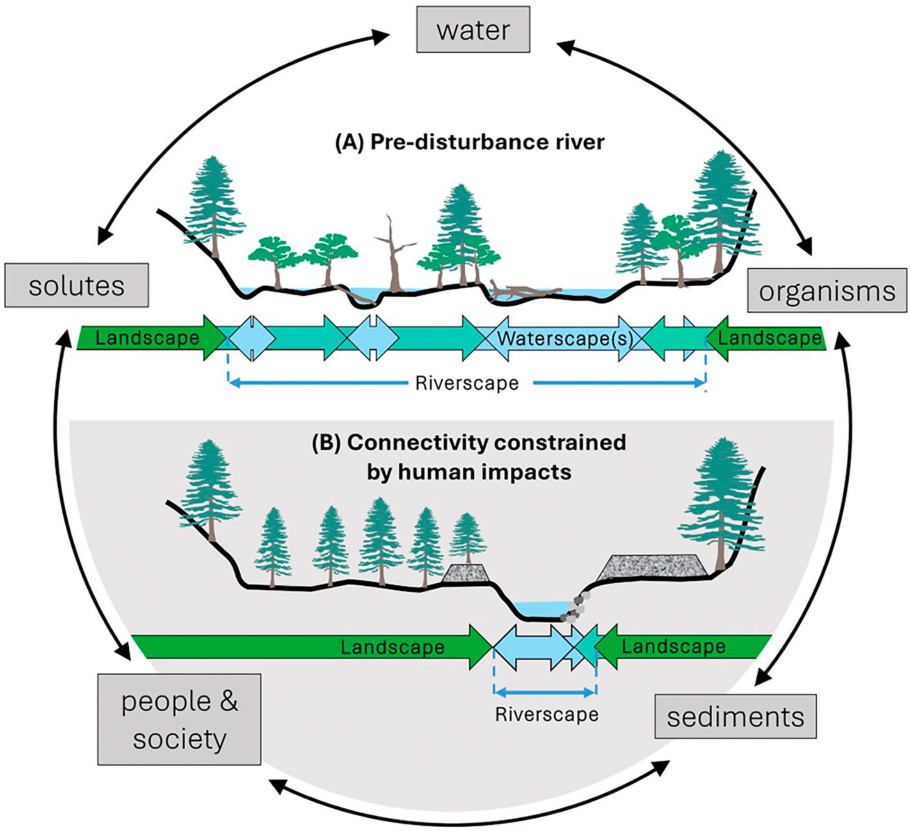

FIGURE 2 | Defining bidirectional lateral connectivity for a pre-anthropogenic disturbance riverscape (A) and a modified riverscape (B). Lateral connectivity describes the movement of many materials (outer circle) within and between waterscapes and landscapes. Event-related and seasonal expansion/contraction of the waterscape(s) drive many laterally connecting processes. The waterscape and the area bidirectionally connected to the waterscape forms the riverscape. Riverscapes have been shrinking globally due to anthropogenic activities. River cross sections adapted from Hogervorst and Powers (2019).

as transitional riverine habitats, or hydrologic ecotones, are characteristically biologically diverse, their reduction contributes to the ongoing collapse in global biodiversity (Krause et al. 2017; Wohl et al. 2021).

In response to anthropogenic modifications to lateral connectivity, there is increasing interest in "reconnecting" rivers to floodplains. Recent experience in river restoration demonstrates the benefits of restoring river–floodplain connectivity to help boost biodiversity (Leigh and Sheldon 2009; Opperman et al. 2009; Beechie et al. 2010; Desjonquères et al. 2018; Wohl et al. 2021), including aiding endangered fish populations (Flitcroft et al. 2022; Stoffers et al. 2022) and increasing the resilience of rivers to the impacts of climate change (Weber et al. 2017; Pugh et al. 2022). It follows that shifting the focus of river research, management, and restoration toward "rebalancing" lateral connectivity should help recover lost riverine biodiversity and ecosystem services, while increasing river resilience in the face of a changing climate (Opperman et al. 2010; Cluer and Thorne 2013; Powers, Helstab, and Niezgoda 2019; Wohl et al. 2021; Flitcroft et al. 2022). Rebalancing connectivity involves reinstating lost and desirable directions of connectivity, where anthropogenic constraints allow, to maximize the societal value and services provided by the riverscape. In most contexts, this involves reducing L ➔ W and restoring W ➔ L fluxes, by slowing material flows into river systems and promoting hydrological fluxes from rivers to landscapes.

In river science and management, there is wide variability in how much emphasis is given to lateral versus longitudinal connectivity. In river management there remains a tendency to view rivers as being, first and foremost, linear (longitudinal) features, which can lead to management and policy approaches that favor longitudinal over lateral connectivity. For example, recent research quantifying the impacts of "physical blockage of free-flowing rivers" only considered structures which primarily restrict longitudinal connectivity (dams, weirs, sluices, culverts, fords, and ramps) (Parasiewicz et al. 2023). Yet physical barriers restrict river lateral connectivity across most rivers globally, including levees, drainage and over-deepened river channels (Chin 2006; Blann et al. 2009; Woodbridge et al. 2016; Gurnell and Downs 2021; Morrison et al. 2023), although these barriers are often less obvious (and their construction less well documented) than weirs and dams. That said, there is an increased focus on restoring lateral processes (Opperman et al. 2009; Beechie et al. 2010; Serra-Llobet et al. 2022), though ambition is often limited to hydrological reconnection at river stages that exceed bankfull, without recognizing the anthropogenic impacts which have modified bankfull or the importance of lateral processes at low flows.

In practice, the ability to identify, conceptualize, and quantify lateral connectivity is important to plan and evaluate river management. This concept has important legal implications. For example, the EU Water Framework Directive applies to aquatic ecosystems and terrestrial ecosystems which "directly depend" on these aquatic ecosystems (Stoffers et al. 2024; WFD; 2000/60/EC) while the EU Biodiversity Strategy requires definition of "free-flowing rivers," including the lateral dimension (van de Bund et al. 2024). Consequently, we require an explicit definition of lateral connectivity in concept and practice, one that identifies how connectivity varies naturally through space and with flow stage and considers ongoing human impacts on lateral connectivity and future management strategies.

In this paper, we review river lateral connectivity with the aim of reframing how this is considered in river research and management. We review knowledge across multiple materials and organisms (e.g., water, solutes, sediments, and biota). We consider lateral connectivity in an anthropogenic context: examining society's impact on laterally connecting processes, the reciprocal impacts of lateral connectivity on society, and how a better understanding of lateral connectivity can be used to improve river management. We lay the foundation for a broader appreciation of the many components of lateral connectivity in rivers, and crucially, the linkages between them. We also move beyond the conceptual, to address how lateral connectivity can be identified and quantified, and how the resulting knowledge can be used to guide restoration of rivers for the benefit of both people and nature. A focus on lateral connectivity forces one to "think outside the channel" and view the drainage network not as comprised of discrete zones (e.g., aquatic, riparian, terrestrial), but as a shifting mosaic of inter-connected elements and patches whose boundaries are fuzzy and change through time and space (Stanford, Lorang, and Hauer 2005). We hope our review will provide a foundation for future, multi-disciplinary research and management of lateral connectivity at scales ranging from the short to the long-term, and from individual reaches to entire drainage systems.

2 | Defining and Conceptualizing Lateral Connectivity

Lateral connectivity is the bidirectional transfer of matter, energy, and organisms between and within waterscapes and landscapes (Figure 2). Since aquatic zones are variable through time, expanding and contracting with discharge, both the waterscape and landscape vary in their areal extent. These lateral expansions and contractions are the catalyst for many connecting processes (Junk, Bayley, and Sparks 1989) and support transitional habitats, which shift from being part of the waterscape versus the landscape over time. The *riverscape* encompasses both the wetted features of the river (e.g., channels) and the area of the landscape which is bidirectionally connected to the river (e.g., influenced by fluvial processes, such as riparian zones and floodplains). In the lateral dimension, waterscapes, riverscapes and landscapes are intimately connected across a range of scales, from the catchment hydrological regime down to the life histories of individual organisms, many of which rely on aquatic-terrestrial connectivity. Thus, a conceptual understanding of lateral connectivity requires consideration of variation through space and time.

Connectivity is commonly divided into two elements: structural and functional (Rinderer, Ali, and Larsen 2018; Wohl et al. 2019). Structural connectivity describes the configuration of the relevant landforms (e.g., the spatial distribution of river channels) and, therefore, how the riverscape and landscape impede or facilitate the movement of matter, energy, and organisms. In contrast, functional connectivity describes the movement of the matter, energy, and organisms themselves. Consequently, structural connectivity can be understood as connectivity in *form* while functional connectivity describes *process*.

2.1 | Conceptualizing Lateral Connectivity in Space

At its most simplistic, lateral connectivity can be understood as the movement of materials, energy, and organisms perpendicular to the river's course (Ward 1989). Of course, the lateral component of connectivity rarely operates in isolation from longitudinal and vertical components (Wohl 2017) and therefore, longitudinal, lateral, and vertical connectivity interact. Increases in the connectivity in one dimension may result in increased connectivity in another. For example, during high flows, sediment is not only moved long-stream but also exchanged laterally, such as via surface runoff, tributaries, and bank erosion and exchanged vertically with the river bed and floodplain (Benda and Dunne 1997; Rice and Church 1998). Many of the processes involved in lateral connectivity also increase vertical connectivity between surface water and subsurface water stores and pathways. Therefore, although our focus is on lateral connectivity, the ideas, concepts, and approaches we present also relate to longitudinal and vertical connectivity.

Rivers occur naturally along a spectrum in the strength and direction of their lateral connections, and the ratio of L ➔ W to W ➔ L fluxes can vary substantially through space (Figure 3A,B). Variations in lateral connectivity with position along river systems have been recognized in several conceptual models. The Fluvial System Model (Schumm 1977) provides a geomorphic perspective on longitudinal changes in sediment sources and transport processes. This model identifies three process domains (Schumm 1977), sediment production, transfer, and deposition zones, which differ in the balance between L ➔ W and W ➔ L fluxes (Figure 3Ci). The River Continuum Concept (Vannote et al. 1980), while emphasizing the longitudinal connectivity of rivers, also incorporates some consideration of lateral connectivity along a river's course (L ➔ W) via terrestrial inputs of organic matter (allochthonous litter) (Figure 3Cii). Viewing the Fluvial System Model and the River Continuum Concept through the lens of lateral connectivity, we suggest broad-scale predictions of lateral dynamics in each process zone (Figure 3Ci,ii). In streams characterized by confined valleys and higher slopes, lateral inputs L ➔ W typically exceed those W ➔ L (Zone 1). For example, surface water and transported sediments, biota and solutes drain directly into channels (and L ➔ W connectivity is not buffered by floodplains). Belowground, lateral connectivity processes are more complex, since in steep headwater streams, hydrologic gains and losses via lateral exchange are common (Payn et al. 2009), although subsurface flows are often predominantly L ➔ W (net gaining reaches). In contrast, rivers characterized by low slopes and wide valleys with extensive floodplains, are characterized by a higher degree of W ➔ L connectivity (Zone 3), since subsurface and surface flows of water (flooding) exchange materials with the

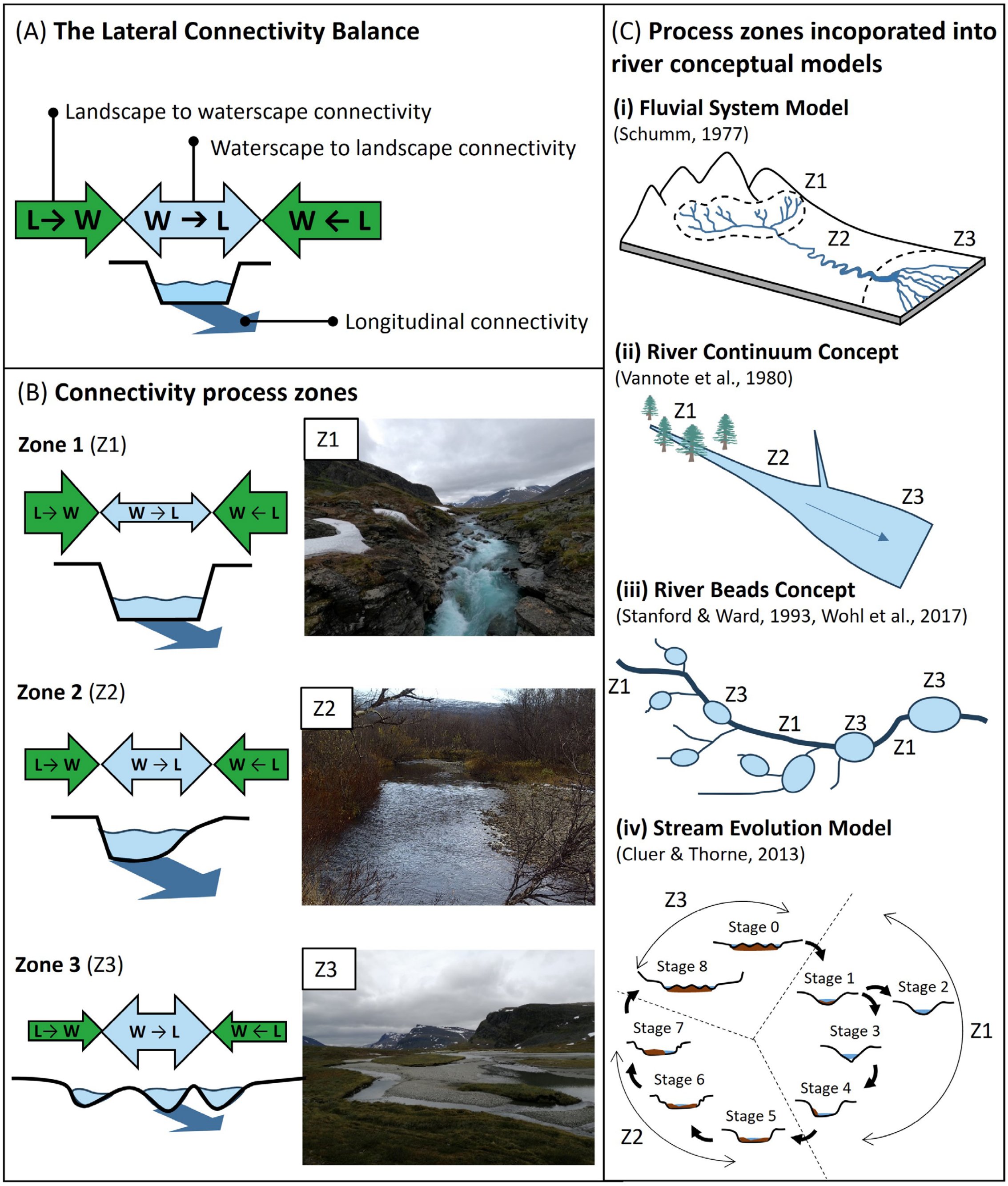

FIGURE 3 | The lateral connectivity balance (A) describes the relative importance of waterscape to landscape (W ➔ L) and landscape to waterscape (L➔ W) fluxes. (B) Three process domains along a continuum of changes in the lateral connectivity balance. Zone 1: rivers dominated by inputs into the waterscape, L➔ W; Zone 2: rivers with similar magnitudes of L➔ W and W ➔ L; Zone 3: rivers characterized by high outputs of material from the waterscape onto floodplains and valley floors. Examples of each process domain reach type may be found in the Torne River drainage system, northern Sweden; (Z1) Šielmmánjira, (Z2) Mjellejohka, and (Z3) Čeavččanjira. (C) The lateral connectivity balance incorporated into four conceptual models to understand spatial and temporal patterns in river processes. The locations of lateral connectivity process Zones 1–3 (from B) are indicated. Image credits: Z1 and Z3, Richard J. Mason. Z2, Sophia Laporte.

floodplain and wider riverscape. In transfer zones, long-stream transport of materials dominates although some lateral exchange with the floodplain occurs (Zone 2).

An important limitation of both the Fluvial System Model and the River Continuum Concept is that they present gradients in processes as smooth and continuous along the river long profile. In reality, longitudinal discontinuities are prevalent in most catchments and can correspond to strong shifts in the balance between longitudinal and lateral connectivity (Montgomery 1999; Poole 2002; Fryirs et al. 2007). Lateral inputs of sediment (e.g., landslides or heavy inputs of sediment from tributaries, Rice and Church 1998; D'Odorico and Fagherazzi 2003), sediments derived from glacial processes (Mason and Polvi 2023), biogeomorphic activities (e.g., log jams or beaver dams; Wohl and Beckman 2014), channel blockages resulting from human activities (e.g., dams and weirs; Ward and Stanford 1983), and variation in valley floor width (Wohl, Lininger, and Scott 2018), may all drive lateral connectivity by increasing residence time and roughness, promoting lateral (and vertical) flows of materials. Consequently, lateral connectivity Zones 1–3 (Figure 3B) are often interspersed along the course of the river and, at the catchment scale, discontinuities in longitudinal connectivity promote spatial variability in the processes driving lateral fluxes and connectivity.

The String of Beads analogy (Stanford and Ward 1993; Wohl, Lininger, and Scott 2018) provides a useful model in many catchments to explain spatial variability in lateral connectivity (Figure 3Ciii). This describes how rivers oscillate with distance downstream between reaches with narrow valley floors (i.e., strings, Zone 1), where the planform is constrained to a single-threaded channel, within which fluvial processes are closely coupled with valley side slope processes and lateral connectivity is dominated by L ➔ W inputs of water, energy and matter, versus reaches with wider valley floors (i.e., beads, Zone 3), where the planform is unconstrained and multi-threaded, fluvial processes dominate and lateral connectivity features both L ➔ W and W ➔ L processes (Fryirs and Brierley 2010; Fryirs, Wheaton, and Brierley 2016; Wohl et al. 2021). The Serial Discontinuity Concept was developed to capture the effects of dams in interrupting longitudinal connectivity (Ward and Stanford 1983). Although the Serial Discontinuity Concept did not initially consider lateral interactions, it was later extended to incorporate lateral flood processes (Ward and Stanford 1995). While dams may increase W ➔ L connectivity upstream through increased material residence time, they may simply move the transition zones (e.g., riparian) in the backwatered reach vertically upwards (and remove natural variability in water elevation in the ponded zone). Similarly, dams may regulate downstream discharges such that lateral fluctuations driving W ➔ L within the downstream waterscape are reduced (Stone, Byrne, and Morrison 2017).

Finally, it is important to note that the conceptualization of lateral connectivity in space is scale dependent. Fluvial systems may be viewed as a nested hierarchy of scales (Frissell et al. 1986; Petts and Amaros 1996; Polvi 2020). At the catchment scale, surface hydrological connectivity depends on landform configuration including the shape and relief of the basin, the topology of the drainage network (Altermatt 2013; Rice 2017). Hydrological connectivity, however, is not confined to the surface river network because fluxes of hyporheic and groundwater also occur (Winter 1999; B. Liu et al. 2022). Similarly, while many organisms use the waterscape to move around the catchment (Rossi et al. 2024), others use the terrestrial and aerial parts of the riverscape or landscape for migration or dispersal (Bunn and Hughes 1997; Lancaster and Downes 2013). At the valley scale, connectivity between hillslope, floodplain, and channel storages governs when, how, and how much material moves into and through the fluvial system. On the valley floor, flood pulses control the degree and direction of lateral connectivity between channels, riparian zones, valley floors, and hill slopes. At the habitat patch scale, the mobile boundaries between the waterscape and the riverscape margins, together with the transitional ecotones they support, provide the links between the aquatic, riparian, wetland, and terrestrial zones, and are hotspots for biogeochemical (e.g., nutrient cycling, contaminant processing), geomorphological (e.g., bank erosion, bar accretion), and ecological processes (e.g., insect emergence, seed germination, and fish population dynamics).

2.2 | Conceptualizing Lateral Connectivity Through Time

Lateral connectivity varies through time. Flow stage is a strong determinant of lateral connectivity, with hydrological pulses driving the connectivity of many materials. Thus, seasonal variation in connectivity is key to river functioning. Temporal variation in lateral connectivity is also highly dependent upon river characteristics. Most work on lateral connectivity has focused on rivers which flood (Zones 2 and 3 in Figure 3). Floodplains are formed by lateral fluxes of sediment that is deposited as the river migrates and avulses. The lateral connections between the river and the valley floor results in the temporary storage of large quantities of sediment, controlling the morphology and character of floodplain environments (Walling et al. 2003; Noe and Hupp 2009; Swinnen et al. 2020). Over annual to decadal timespans, fluctuations and trends in the hydrological regime drive considerable variability in both the direction and magnitude of laterally connecting processes. Therefore, while for most of the year, river channels act primarily as sinks for materials and energy from the wider catchment, during high flows, flooding drives bidirectional exchanges (Figure 4). In contrast, reaches in more confined valley segments (Zone 1 in Figure 3), and rivers that have incised sufficiently to disconnect their channels from their floodplains, primarily flush material downstream during high flows.

The Flood Pulse Concept (Junk, Bayley, and Sparks 1989) was developed to understand seasonal changes in lateral connectivity in rivers with floodplains. This concept describes connectivity driven by the expansion and contraction of the waterscape, due to changes in river stage and was foundational in recognizing that flood pulses drive both L ➔ W and W ➔ L lateral connectivity, iv and that materials derived from the floodplain are critical to both floodplain and in-channel processes. Furthermore, disturbance resulting from flood pulses maintains dynamism in floodplain processes. While the Flood Pulse Concept was originally developed for large tropical rivers with extensive periods of flooding (Junk, Bayley, and Sparks 1989), Tockner, Malard, and Ward (2000) extended the model to temperate systems, specifically detailing the importance of discharge pulses that occur below bankfull stage. The resulting Flow Pulse Concept is therefore better suited to many human-modified rivers that rarely flood. The Flow Pulse Concept emphasizes that as discharge increases, but remains below bankfull, lateral expansion is nonetheless important in connecting diverse habitats inset below the valley floor. such as paleo-channels and disconnected anabranches (Tockner, Malard, and Ward 2000). However, in overly simplified anthropogenic channels, high discharges, which remain below bankfull, may lead to increased depths and velocities with little increase in surface lateral connectivity.

Clearly, the magnitude, timing, and frequency of flood peaks are critical to floodplain inundation and lateral connectivity.

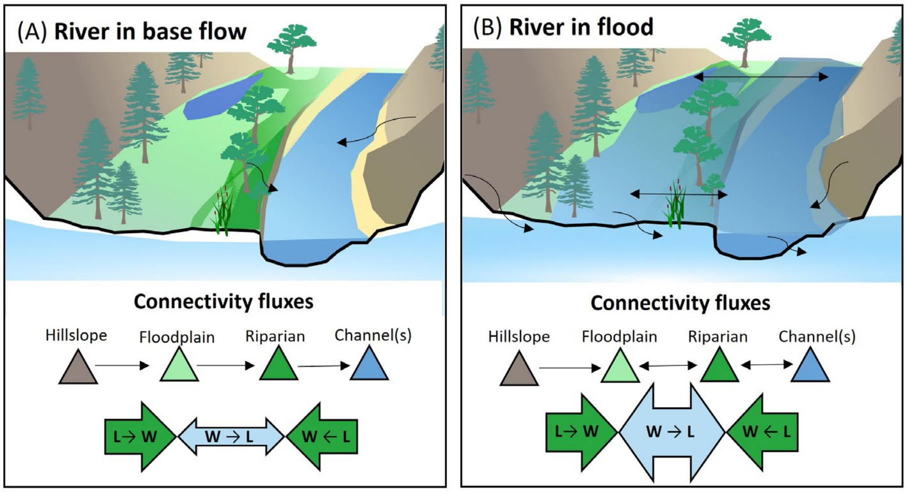

FIGURE 4 | Lateral connectivity is strongly dependent on season and discharge; at base flow (A), this hypothetical river is dominated by landscape to waterscape (L ➔ W) fluxes, because water flows into the river from tributaries, as surface runoff and via the hyporheic aquifer. During high flows (B), the floodplain is inundated, and net fluxes of water, sediments and biota occur from the waterscape into the riverscape and adjacent landscape (W ➔ L).

This is recognized in the Natural Flow Regime Concept (Poff et al. 1997), which explains how key aspects of hydrographs (magnitude, frequency, duration, timing, and flashiness) impact river ecosystems, and how human modifications to river discharge that produce unnatural flow regimes, degrade river ecosystems, disproportionately affecting native species that have co-evolved with naturally variable flows. Allen et al. (2020) draw attention to the importance of connectivity in non-perennial rivers. Even during periods when surface water connectivity is interrupted, lateral connectivity may continue (e.g., via wind, animal movement). In their recent "foodscapes for salmon" concept, Rossi et al. (2024) provide a template for understanding the importance of connectivity between resources in the waterscape. Mobile consumers, like salmon, can track fluxes in resources such as food, shelter, or rearing habitats, thus access to zones of different lateral connectivity (i.e., Zones 1–3 in Figure 3) is important at different life stages.

The River Wave Concept (Humphries, Keckeis, and Finlayson 2014) seeks to integrate existing frameworks and is anchored by the notion that these different concepts operate under specific flow conditions. For example, the River Wave Concept suggests that the relative importance of autochthonous and allochthonous production (and therefore the importance of L ➔ W connectivity) differs with flow stage. At low flows the Riverine Productivity Model (Thorp and Delong 1994) best captures the transformation and storage of materials within the channel and local inputs of allochthonous materials, while at medium flows the River Continuum Concept (Vannote et al. 1980) best explains the importance of longitudinal matter transport, and at peak flows, ecosystem dynamics are best captured by the Flood Pulse Concept (Humphries, Keckeis, and Finlayson 2014). Thus, the relevance of each concept depends upon the landscape setting and flow stage of a river.

An important limitation of these concepts is that they take little account of channel morphology and, in particular, human modification of river channels. The same magnitude flood will have different impacts on lateral connectivity depending upon river type and channel morphology. The Stream Evolution Model (Cluer and Thorne 2013; Figure 3Civ) describes changes to channel morphology through time, resulting from disturbances, such as those caused by anthropogenic activities. Considering the Flood Pulse Concept and Flow Pulse Concept at different stages of the Stream Evolution Model clearly shows the influence of channel cross-section morphology on lateral connectivity under different discharge scenarios (Figure 5). Anastomosing rivers (Stages 0 or 8 of the Stream Evolution Model) have a gradation of lateral features that are sequentially submerged by rising water levels (Figure 5a). The anthropogenic simplification of lateral topography, particularly of floodplains, has led to lateral connectivity becoming more binary, with the flow being above or below bankfull, as opposed to a gradient of connectivity as flow magnitude increases. In degrading channels (Stages 1–4), increasingly large floods are contained within the channel (Figure 5B). Such flows flush matter and organisms downstream, earning them the epithet "fire hose channels" (Johan Hogervorst, pers. comm., 2016) and flow events that inundate the former floodplain (which has become a terrace) are relatively rare.

3 | Lateral Connectivity Involves Water, Sediments, Solutes, Organisms, and Society

Lateral connectivity provides an informative and interdisciplinary lens through which to view hydrological, geomorphic, biogeochemical, ecological, and social processes and, crucially, the linkages between them (Figure 2). Connectivity of many of these materials is driven by hydrological processes but other drivers of transport occur, including eolian and gravity-driven processes, and the active movements of animals. Here we provide a summary of the lateral connectivity of each material type and how it influences, and is influenced by, other material fluxes.

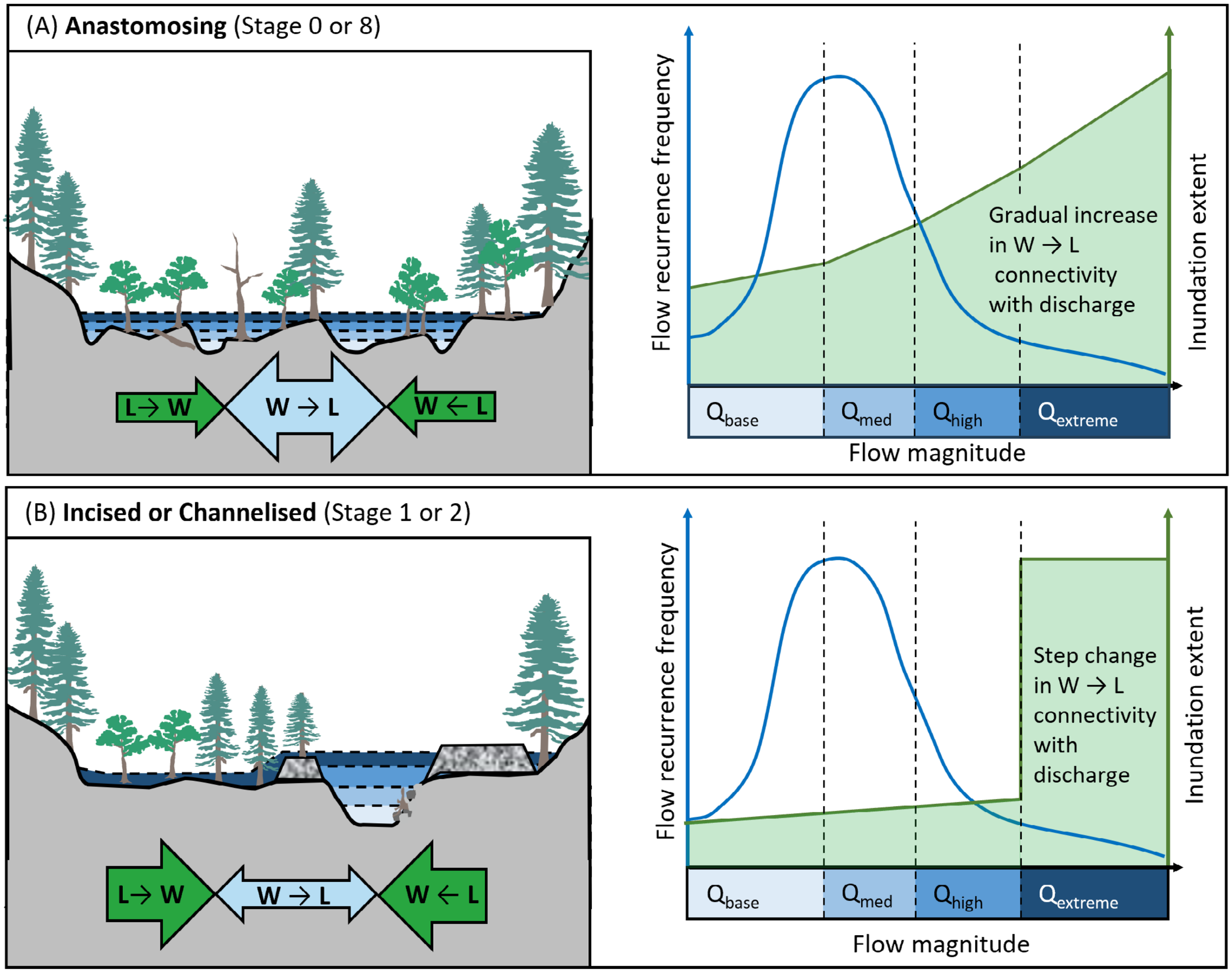

FIGURE 5 | Influence of channel morphology on lateral connectivity under different discharges. As the flow stage increases in the anastomosing river–wetland complex (A) an increasing proportion of the valley floor surface and activating floodplain features are wetted, resulting in a gradual increase in W ➔ L lateral connectivity processes. In contrast, the incised, single-thread channel (B) switches from connected only L ➔ W to connected W ➔ L abruptly when the flow depth exceeds bankfull, as demonstrated by Wolman and Miller (1960).

3.1 | Water

Hydrological connectivity is of primary importance since it drives the connectivity of many other materials and organisms. The degree of hydrological connectivity is controlled by multiple factors including the hydrograph and the landform configuration. At the network scale, catchment shape and river network topology determine the degree of L ➔ W connection (Rice 2017; Heasley, Clifford, and Millington 2019). L ➔ W is further mediated by surface topography, vegetation, artificial infrastructure, and animal activities, all of which may increase or slow the flow entering the drainage network. Hydrological connectivity between regional groundwater and the waterscape is controlled by the hydraulic conductivity of the aquifer, and the hydraulic gradient, which, while influenced by topography, may not follow surface flow paths (Condon and Maxwell 2015). These factors all control the rate at which water reaches river channels, and thus the discharge hydrograph. The hydrograph, in turn, has a strong influence on downstream lateral W ➔ L connectivity since it is a key control on flood magnitude, frequency, and duration.

Below the surface, hydrological exchange flows act both laterally and vertically between river channels, hyporheic zones, and groundwater. The hyporheic zone is defined as the area in which water moves through sediments and returns back to the river channel, resulting in bidirectional transfers (Gooseff 2010). In contrast, groundwater exchanges are typically larger in spatial scale and unidirectional (Boano et al. 2014). Hyporheic flow is often envisaged as a vertical transfer but horizontal transfers are equally important (Poole et al. 2008). Hyporheic flow is driven by energy gradients at, and just below, the riverbed (Boano et al. 2014), and thus stream slope, stream bed topography and sinuosity are critical for vertical and lateral hydrological exchanges (Poole et al. 2008).

3.2 | Solutes, Gases, Organic Resources, and Pollutants

Water flow paths exert strong controls over the transport of dissolved gases, solutes, and particulate organic matter, all of which may influence the ecological and biogeochemical functioning of riverscapes. As described by Poole et al. (2008), flow paths, often stretching 100 m laterally, "knit together" riverine ecosystems. Thus, transfers of nutrients and solutes occur both L ➔ W and W ➔ L and are essential for the functioning of habitats and the ecotones that rely on them, providing energy as well as the elemental building blocks that support stream and riparian food webs (Meyer et al. 1988). Lateral transport of a given solute L ➔ W from soils to streams is sensitive to the vertical location of its storage in soils, relative to the elevation of the water table (Li et al. 2024). Differences in vertical storage across solutes can thus give rise to distinct mechanisms and patterns of lateral mobilization with changing discharge due to variations in water table elevation (e.g., transport vs. supply limitation; Mosquera et al. 2023). Lateral mobilization is also notably sensitive to land-use activities (e.g., fertilizer application) and climate features that either directly alter the amount and vertical distribution of resource pools in soils (Moatar et al. 2017) and/or modify the vertical position and dynamics of hydrologic flow paths that drain soils (Li et al. 2024).

Considerable research has also focused on lateral exchanges between larger rivers and their floodplains, both above and below ground. As the area of the connected floodplain often far exceeds that of the river channels, floodplains can be particularly important sources of resources L ➔ W, which may exceed what is produced locally or supplied from upstream sources (e.g., Cuffney 1988). Yet, sediment deposition can be an important mechanism for transferring nutrients from channels to floodplains W ➔ L, particularly for phosphorus (Noe and Hupp 2009). Similarly, given the potential of floodplains to support anoxic soils and wetlands, lateral transfer of nitrogen W ➔ L can result in significant reductions of nitrate through denitrification (e.g., Forshay and Stanley 2005). Finally, hydrological connectivity between channels and floodplains during flood pulses can supply oxygen to connected aquatic habitats, which is critical for aquatic communities (e.g., Winemiller and Jepsen 1998; Starr, Benstead, and Sponseller 2014). However, floodplain soils and wetlands also have an enormous capacity to consume oxygen, and a high degree of W ➔ L connectivity can result in severe oxygen depletion of river channels (Zurbrügg et al. 2012), in some cases with negative ecological consequences (e.g., fish mortality; Hamilton et al. 1997). Similarly, floodplains may act as stores for river-derived pollutants which may be remobilized during periods of enhanced L ➔ W connectivity (Lair et al. 2009), though floodplains generally also process pollutants and can reduce their overall availability (Gordon, Dorothy, and Lenhart 2020).

In addition to acting as a vector that carries particles, solutes and gases, hydrologic flow paths also influence the lateral exchange of matter by integrating biogeochemically active interfaces between land and water, and surface and groundwater (Krause et al. 2017). Indeed, hydrological flows often connect patches within the fluvial landscape that support different physical, biogeochemical, and microbial characteristics. Transitions between these patches can support sharp gradients in conditions (e.g., in sediment redox), which drive locally high rates of biogeochemical processes that either produce or remove a range of solutes (McClain et al. 2003; Krause et al. 2017). These *hotspots* or *control points* (Bernhardt et al. 2017) can have disproportionately large effects on the mass flux of dissolved materials moving across the broader landscape and can thereby act to either enhance or limit biological processes within recipient patches (Vidon et al. 2010; J. Harvey and Gooseff 2015). In this way, the lateral exchange of materials can be greatly influenced by the capacity for biogeochemical transformations to occur along hydrological flow paths, which is in turn related to the medium through which water moves and the types of patches and interfaces that are integrated within the riverscape (Fisher and Welter 2005).

3.3 | Sediment

The connectivity of sediment will in many cases map onto the hydrological connectivity, where sediment is available to be transported and the hydrological network has sufficient power (Hooke 2003). However, sediment connectivity also includes non-fluvial processes that may be independent of the hydrological drainage network (e.g., landslides or eolian transport), which together yield a network of sedimentary links and nodes that overlies, but is not entirely equivalent to, the catchment-scale hydrological drainage network (Rice and Church 1998; Rice 2017). Fryirs et al. (2007) conceptualize sediment connectivity as a series of switches which control sediment delivery. In return, sediment connectivity controls hydrological connectivity across many scales, as sediment volume and caliber combine to determine channel morphology (Church 2006). Lateral erosion and sediment deposition within the channel, for example, drives river meandering (Dietrich and Smith 1984; Russell et al. 2018). Channel morphology then has a strong influence on overbank flows and W ➔ L connectivity: in particular, channel capacity (Figure 5) and channel roughness (Cienciala et al. 2020). At a smaller scale, fine sediment in interstices controls hyporheic hydrological (Negreiros et al. 2023) and biological (Mathers et al. 2019) connectivity.

There has been a strong research focus in geomorphology on L ➔ W connectivity, including hillslope erosion and channel coupling (A. M. Harvey 2002), and fine sediment transport into the channel network (Naura et al. 2016; Poeppl et al. 2019). W➔ L sediment connectivity is also important, since it controls floodplain formation and channel migration (Ashworth and Lewin 2012). Floodplain construction with sediment delivered from active channel(s) controls floodplain stratigraphy, hydraulic conductivity, and erosional resistance, which in turn influence subsurface water and solute fluxes, and the ecological communities and biogeochemical dynamics that control floodplain functions (Wohl 2021). After residing in the floodplain for tens to thousands of years (Wohl 2015), the sediment can be returned to the active channel via bank or floodplain surface erosion (Dunne et al. 1998). Floodplain budgets (Wohl 2021) describe the balance between L ➔ W and W ➔ L sediment transport and the resulting aggradation or degradation of floodplains.

3.4 | Biota

Many organisms may move both actively and passively between the waterscape and landscape. Benthic invertebrates (Petersen et al. 2004), fishes (Olden, Jackson, and Peres-Neto 2001; Dias et al. 2013), and plants (Schmiedel and

Tackenberg 2013) use stream corridors for dispersal by crawling, swimming and drifting. Many wind-dispersed plants, crayfishes, amphibians, and emergent flying adult insects may instead disperse over land (Bunn and Hughes 1997; Lancaster and Downes 2013). Depending upon their modes of dispersal, the constraints and opportunities afforded to their movement will vary (Tonkin et al. 2018). At the network scale, species that disperse within riverine corridors are likely to be more influenced by the structure of the network compared to those that disperse over land. As a result, the dendritic structuring of rivers can be a primary determinant of animal and plant distributions (Johansson, Nilsson, and Nilsson 1996; Muneepeerakul et al. 2008).

Bidirectional lateral connectivity between channel and floodplain habitats is crucial in the lifecycle of many organisms across a range of time scales. Many fish commonly use secondary channels, floodplain wetlands (e.g., Rosenfeld and Carrier 2008), or ponds (Couto et al. 2018) and connectivity between these habitats is essential (Stoffers et al. 2021). For example, some fish species travel daily between main channels and floodplain habitats to reach areas with optimal temperatures (Bischoff and Scholten 1996), avoid predators (Baras and Nindaba 1999), or feed (Tewson et al. 2016). Furthermore, many species of fish spawn on the inundated floodplain (Górski et al. 2010; Stoffers et al. 2022). Therefore, biological connectivity is often mapped onto specific temporal or seasonal patterns in hydrological lateral connectivity (Naiman et al. 2008; Erös et al. 2012). Similarly, many species of riparian plants have evolved to release their propagules during periods of peak flow, relying on flows within the riverscape or frugivorous fish, to disperse the propagules (J. T. Anderson, Rojas, and Flecker 2009; Nilsson et al. 2010). Thus, the direction and nature of lateral connectivity varies through time and organisms must adapt to utilize different areas of the riverscape as discharge varies (Rossi et al. 2024).

The transitional riparian zone is critical for both aquatic and terrestrial biota. Riparian vegetation provides shade, with implications for stream temperature (Johnson and Wilby 2015) and animal behavior (Sabal et al. 2021). Riparian vegetation also provides inputs of organic material, altering stream communities (Vannote et al. 1980). In-channel vegetation influences hydraulic roughness (Manners et al. 2013; White et al. 2023), providing structure and habitat diversity. Such structures are used by aquatic biota, including zooplankton, invertebrates and fish for refuge, grazing, and attachment (Angermeier and Karr 1984; Negishi, Inoue, and Nunokawa 2002). For example, many insects will use emergent structures at channel margins to crawl from the water, emerging as terrestrial adults that reproduce and lay eggs back into the water (Lancaster and Downes 2013). River banks are also important habitats for many burrowing species (e.g., crayfish; Sanders et al. 2023). As a result, rivers provide essential structural, energy, and nutrient resources for terrestrial food webs and vice versa (Nakano and Murakami 2001).

Organisms exert strong feedback effects on other laterally connecting processes. For example, terrestrial vegetation affects river hydrographs by influencing surface roughness and infiltration rates (e.g., Crockford and Richardson 2000), the stability of regolith and rates of weathering of bedrock (e.g., Pawlik, Phillips, and Šamonil 2016), and subsurface water content via transpiration (Stoy et al. 2019). Paths and channels eroded by animals can increase L ➔ W connectivity and increases habitat complexity (Naiman and Rogers 1997). Similarly, the animals themselves provide pathways for the transport of nutrients. For example, hippopotamuses convey carbon and nutrients L ➔ W via excrement (Sabalusky et al. 2015), salmon provide a nutrient source for riparian forests (e.g., W ➔ L; Helfield and Naiman 2001), and the emergence of aquatic insects provides prey subsidies for terrestrial consumers (Richardson and Sato 2015). Within the river channel, biogeomorphic processes are also important controls on the connectivity of all constituent materials, including water (e.g., beaver, Larsen, Larsen, and Lane 2021; invertebrates, Mermillod-Blondin 2011), sediment (e.g., fish & invertebrates, Rice, Johnson, and Reid 2012; Mason and Sanders 2021), and solutes (e.g., invertebrates; Mermillod-Blondin and Lemoine 2010). Thus, an appreciation of biological power is key to connectivity and therefore river management (Johnson et al. 2019, 2024).

3.5 | People and Society

Connectivity with water has been a primary influence on cultural development, livelihoods, identity, sense of place, and religion (Boelens 2014; E. P. Anderson et al. 2019). Rivers have a strong influence on the movement of people and goods, both enabling and restricting movement. For example, dispersal corridors within river networks likely facilitated the migration of humans out of Africa 120,000 years ago (Osborne et al. 2008). In contrast, rivers often mark the edges of territories since they provide natural barriers to the lateral connectivity of people and cultures (Axelsson, Sköld, and Röver 2019). Furthermore, riverine connectivity supports society by providing a vast range of primary products and ecosystem services. Since the earliest human civilizations, floodplain ecotones have been shared spaces for people and the river, due to the advantages of social connectivity to waterscapes (Petsch et al. 2023). Specific timings of lateral connectivity have been used by people (Wantzen et al. 2016). For example, the lower Mekong flood pulse (Junk, Bayley, and Sparks 1989) is essential to fisheries as well as many other floodplain services (Grundy-Warr and Lin 2020). Consequently, social connectivity to riverscapes is essential for livelihoods, has been of significant importance in the development of culture, and is important to society today.

However, historically there has been a tendency to view water resources independently from their cultural and social values (E. P. Anderson et al. 2019). For example, excluding human management from river conceptual models (Abbott et al. 2019; Wymore et al. 2023), yet such context is critical for river management. In river science, the importance of people as an intrinsic part of the water cycle is recognized in disciplines of social hydrology (Sivapalan et al. 2014; Pande and Sivapalan 2017; Wesselink, Kooy, and Warner 2017) and the hydrosocial cycle (Boelens 2014). Increasingly, river management is incorporating not only the biophysical sciences but also society and culture (Boon 1998; Pahl-Wostl, Gupta, and Petry 2008; E. P. Anderson et al. 2019). Connectivity to riverscapes is especially important in urban areas where rivers are more likely to be viewed through a primarily negative lens (Cervantes-Avilés, Mares, and

Osorno-Sánchez 2024). May (2006) state that, for urban planners, connectivity to rivers involves accessibility (pedestrian paths, bridges, and transport), visual and cultural links to the city (e.g., greenways, attractive river margins) and cultural attractions at the river edge. Such connectivity is often lost through traditional hard engineering approaches such as levee construction, which may remove physical and visual access to riverscapes and degrade transitional ecotones like riparian zones and floodplains. Yet, with thoughtful design, beneficial aspects of social connectivity to riverscapes can be maintained and restored, even in constrained urban settings (Mathias Kondolf et al. 2018).

Restoration of social connectivity may determine the perception of success for a restoration project (Kondolf and Pinto 2017) and integrating social goals alongside physical and biological functionality is essential to restore river ecosystem services. River restoration should not only aim to consider the views of community and civil groups but also be led by these groups (Smith, Clifford, and Mant 2014), installing senses of guardianship and thus ideological connectivity to the river. Furthermore, the greatest challenges to restoring floodplain connectivity are social (e.g., regulatory or perceptions) rather than technical (Serra-Llobet et al. 2022). However, this poses challenges for the restoration of lateral connectivity. For example, public perception often views rivers and valley floors as separate, discrete entities and bidirectional lateral connectivity as a predominantly negative process. Challenging this perception is key to rebalance lateral connectivity.

4 | Identifying and Quantifying Lateral Connectivity in Practice

Moving from an abstract concept to identifying and measuring connectivity is a challenge. This is due to many factors including the lack of consensus about the definition of connectivity and the practical complexity of measuring the many, interacting, processes involved. Furthermore, the time period for which lateral connections are visible is commonly short-lived and can be unpredictable (e.g., floodplain inundation or insect emergence). Nevertheless, quantifying lateral connectivity is important for understanding the interactions between aquatic and terrestrial zones, for comparing levels of lateral connectivity between sites, and for designing and assessing the outcomes of river management and restoration projects.

Table 1 provides an overview of methods used to assess lateral connectivity, with respect to water, solutes, sediments, biota, and people. Lateral connectivity has a long history of study; however, most studies consider a single aspect of connectivity and choose a measure aligned with this purpose, in isolation from other aspects of connectivity. Consequently, the interactions between different connecting processes remain poorly understood and research at this interface is required to develop a deeper understanding of river systems (Gallardo et al. 2009; Trigg et al. 2013; Wohl et al. 2019).

Assessments of structural connectivity are typically easier to make than those of functional connectivity and so the former is often used to infer the latter. Hydrological lateral connectivity of channel and floodplain aquatic habitats may be assessed by measuring floodwater inundation extents (e.g., satellite imagery; Bellido-Leiva, Lusardi, and Lund 2022). However, they may also be inferred from form, such as by modeling flood extents (e.g., Bolland et al. 2012; Beck et al. 2019; Czuba et al. 2019) or by defining a qualitative gradient of connectivity. For example, Manfrin et al. (2020) categorized waterbodies as (1) main channel, (2) permanently connected, (3) occasionally connected or (4) nearly isolated from the main channel. Structural hydrological connectivity may also be inferred from connectivity of other materials and organisms; for example, the biotic community (e.g., vegetation; Akasaka and Takamura 2012) or soil properties (Bourgault et al. 2017).

Large spatial and temporal scales provide a challenge in the measurement of functional connectivity since measuring process is difficult at larger scales. Plot-scale measurements have been the focus for runoff and infiltration studies but are now being upscaled to catchments (Masselink et al. 2016). Tracing both water and sediment (e.g., fingerprinting; Pfister et al. 2009; Guzmán et al. 2013) enables identification of sources for these materials and therefore facilitates measurements of functional connectivity at larger scales. Emerging technologies and data are also facilitating the assessment of connectivity at greater scales than previously possible. For example, high-resolution topographic data facilitates assessment of variability in valley confinement at network scales (O'Brien et al. 2019), while satellite imagery allows floodplain integrity to be assessed at national scales (Morrison et al. 2023) and river channel belts at global scales (Nyberg et al. 2023). Such data are typically limited in their capacity to indicate functional connectivity, but much can be inferred from form.

Given the increased interest in restoring lateral connectivity at both high and low flows (e.g., Figure 5; Flitcroft et al. 2022; Clarke 2024) a key area of future research should be the development of indices describing lateral connectivity that incorporate connectivity of multiple types of matter, energy, and organisms, which can be used across studies and between sites, and can inform conceptual and quantitative modeling of lateral connectivity (sensu Keesstra et al. 2018; Wohl et al. 2019). This is necessary to understand how the outcomes of projects aiming to rebalance lateral connectivity are monitored and evaluated. In this manner, the lateral connectivity balance concept can be used to assess the balance of L ➔ W and W ➔ L in a qualitative or semi-quantitative sense by identifying the fluxes of materials in each direction and assessing their magnitude and frequency of connection. This allows lateral connectivity to be compared between sites or over time (Box 1 and Figure 7).

5 | Restoring and Rebalancing Lateral Connectivity

Systematic and widespread anthropogenic changes to the lateral connectivity of waterscapes and landscapes have typically increased L ➔ W connectivity at the expense of W ➔ L. In many cases, reductions in W ➔ L lateral connectivity result in positive feedback loops; for example, flows that were formally spread across the floodplain are increasingly concentrated within the channel, which increases unit stream power and local sediment transport capacity. Bed scouring can then

TABLE 1 | Summary of techniques used to infer and measure lateral connectivity for different materials.

(1) Water
Stream and tributary network flow paths • Inferred from the spatial distribution of river networks and landscape characteristics (e.g., from digital elevation models; Roelens et al. 2018). • Hydrological fingerprinting, using existing biogeochemical characteristics to identify sources of water and flow pathways within a catchment (e.g., isotopes or diatoms; Pfister et al. 2009; Ala-aho et al. 2018). • Mapping flow pathways by tracking added tracers (e.g., salt or dye; Sparacino et al. 2019; Ader et al. 2021). • Surface and groundwater connectivity inferred from time series analysis of water-level sensors (e.g., Jaeger and Olden 2012), which may also be combined with numerical modeling (Nippgen, McGlynn, and Emanuel 2015; Rinderer, van Meerveld, and McGlynn 2019). **Valley floor habitats and channel connectivity** • Inferred from extent of intact valley bottom (i.e., not blocked by infrastructure; O'Brien et al. 2019; Morrison et al. 2023; van de Bund et al. 2024). • Measured flood extents (e.g., from satellite imagery; Bellido-Leiva, Lusardi, and Lund 2022) and signs of overbank flows (e.g., floodplain sedimentation, flattened vegetation; D. N. Scott 2024). • Inferred from vertical or horizontal distance between channel and possibly connected habitats (e.g., Bolland et al. 2012; Górski et al. 2013; Manfrin et al. 2020; Stoffers et al. 2021). • 1D, 2D, and 3D modeling (e.g., Clilverd et al. 2016; Czuba et al. 2019; Federman, Scott, and Hester 2023). Modeled connectivity can then be compared to historical modeled connectivity (e.g., Eder et al. 2024). • Calculated from hydrographs and morphology (e.g., D. T. Scott et al. 2019; Džubáková et al. 2015). • Inferred from vegetation communities (e.g., Polvi, Wohl, and Merritt 2011; Caskey et al. 2015) or microbial and geochemical indicators (e.g., Brooks et al. 2022). **Overland flow and infiltration** • Assessed via plot-scale measurements (e.g., rainfall simulators, infiltrometers or topography; Wolstenholme et al. 2020). • Inferred from measured floodplain water table (e.g., groundwater wells; Munir and Westbrook 2021). • Models and indices developed to describe connectivity, using a combination of topography and flow dynamics. For example the relative connectivity index (modeled functional and structural connectivity of drylands; Turnbull and Wainwright 2019), all direction flow length, (Mayor et al. 2008), and the topographic over field capacity index (J. Liu et al. 2020).
(2) Solutes, gases, organic resources, and pollutants
Flux between waterscapes and landscapes • Remote sensing to indicate ecosystem functioning (Gardner et al. 2021) (e.g., use of color to estimate dissolved organic carbon; Del Castillo and Miller 2008). • Direct measurements of fluxes (e.g., drift nets to capture mobile particulate organic matter; Tockner et al. 1999). • Measurements of the properties of mobilized material (e.g., sampling floodplain-deposited sediment for carbon, phosphorous, and nitrogen; Noe and Hupp 2005). • Modeling flux between floodplains and channels based on discharge, solute concentration, and floodplain characteristics including trapping efficiency (e.g., for total phosphorous and suspended sediments; Beck et al. 2019). • Mixing models and mass transport models to estimate hydrologic exchange between waterscapes and landscapes and residence times (e.g., transient storage models; J. Harvey et al. 2019). • Tracing land–water fluxes of materials based on chemical signatures (e.g., Stewart et al. 2022). • Variation in concentration through space or time to estimate inputs, exports or processing (e.g., dissolved organic carbon; Moody et al. 2013).
(3) Sediments
Sediment networks • Identifying sediment paths via sediment fingerprinting, comparing properties of in-channel sediment samples to those of potential sources, including tracing via radioisotopes and radionuclides (e.g., Froger et al. 2018; Birkel et al. 2022). • 1D, 2D, and 3D Modeling at network to reach scales (e.g., Schmitt et al. 2016; Heckmann et al. 2018; Gilbert and Wilcox 2020). • Determined from distribution of landforms resulting from lateral sediment connectivity (e.g., alluvial fans; Fryirs et al. 2007).

(Continues)

TABLE 1 | (Continued)

(3) Sediments

Hillslope-channel coupling
- Inferred from valley shape (e.g., valley bottom width; May et al. 2013).
- Mapping of sediment stores and sources (e.g., A. M. Harvey 2002; Schrott et al. 2003; Fryirs et al. 2007).
- Modeling of landslides, rockfalls, and debris flow inputs (e.g., Heckmann and Schwanghart 2013; Prajisha, Achu, and Joseph 2023).

Exchange between channel and floodplain
- Repeat topographic surveys to deduce volumetric changes (e.g., J. M. Wheaton et al. 2010).
- Monitoring of individual plots for erosion or deposition (e.g., Parsons 2019).
- Sediment trapping on the floodplain (e.g., accretion mats; Noe and Hupp 2009).
- Floodplain trapping factor (gross: floodplain yield/stream sediment yield, net: floodplain deposition—bank erosion; Schenk et al. 2013).
- Reconstructed accretion rates and historical connectivity from floodplain sediment stratigraphy coupled with dating (e.g., Hoffmann et al. 2007; Hobo et al. 2010).
- Modeling of channel and floodplain sediment transport potential (Sumaiya et al. 2021).

Channel migration and bank erosion
- Lateral movement of channel through time as measured from remote imagery (e.g., Richard, Julien, and Baird 2005; Dixon et al. 2018; Nagel, Darby, and Leyland 2023) or historical maps or photographs (e.g., J. M. Hooke 1984).
- Erosion and deposition determined from repeat surveys of cross sections (e.g., Lawler 1993), terrestrial lidar scanning (Lyons et al. 2015), photogrammetry, or erosion pins (e.g., Jugie et al. 2018).
- Tracer particles (e.g., maps of traced particles to capture lateral as well as longitudinal movements, Papangelakis and Hassan 2016; magnetic tracing of fine sediment, Milan and Large 2014).

(4) Biota

Movement of animals
- Tracking individual animals via passive integrated transponder technology, acoustic telemetry, biologgers (e.g., Cooke et al. 2013), or videos (e.g., Lancaster et al. 2006).
- Inferred from hydrological connectivity (e.g., Cote et al. 2009) and absence of barriers (e.g., levees or weirs restricting fish passage; Timm et al. 2019).
- Trapping using directional nets (e.g., fish: Górski et al. 2014; invertebrates: Brooks et al. 2020).
- Adult aerial dispersal of aquatic insects estimated with traps/experiments (Bogan and Boersma 2012; Lancaster et al. 2024) or isotopic tracers (Macneale, Peckarsky, and Likens 2005).
- Inferred from otolith chemistry, comparing the elemental and isotopic composition of fish to water characteristics (e.g., Gillanders 2005; Winemiller et al. 2023).

Movement of plants
- Trapping mobile propagules (e.g., Cubley and Brown 2016) or propagule surrogates (e.g., Su et al. 2019).
- Large wood transport monitored from aerial imagery (e.g., Latterell and Naiman 2007; D. N. Scott 2024), field surveys (e.g., Wohl et al. 2024), or modeling (e.g., Steeb et al. 2023).

Connectivity between populations
- Inferred from estimated gene flow of target organisms (e.g., Comte and Olden 2018) or similarity of ecosystem species composition or traits (e.g., Rodríguez and Lewis Jr. 1997).

(5) People and society

Risk
- Flood risk mapping and measurements (e.g., Mudashiru et al. 2021).
- Drought risk modeling and measurements (e.g., West, Quinn, and Horswell 2019; Brunner et al. 2021).

Resource use and access
- Irrigation and water use mapping (e.g., Conrad et al. 2007).
- Visual and spatial accessibility to river (e.g., pedestrian network, height of adjacent buildings, road and public transport accessibility; Kondolf and Pinto 2017; Hermida et al. 2019).
- Continuity of the green space or riverscape (e.g., May 2006).
- Public knowledge and perception of riverscapes (e.g., via interviews and focus groups; Eden and Bear 2011; Spink et al. 2010).
- Data from social media and GPS tracking apps (e.g., Hale, Cook, and Beltrán 2019; Grzyb and Kulczyk 2023).
- Knowledge exchanges and co-development of management strategies (e.g., Fox et al. 2017).
- Combinations of metrics, such as the Urban River Sustainability Index (Hermida et al. 2019).

Note: This table is not comprehensive since most measurements of river form or process include some aspect of lateral connectivity, but it provides a starting point for those looking to measure connectivity processes between waterscapes and landscapes and especially to compare multiple aspects of connectivity.

further deepen the channel, destabilizing its banks and leading to rapid widening (Schumm, Harvey, and Watson 1984; Simon and Hupp 1987; Cluer and Thorne 2013). Once formed, such channels are often locked in place by the encroachment of vegetation (often invasive; Pollen-Bankhead et al. 2009; Wieting et al. 2023) which stabilizes banks and reduces the ability of the river to modify its planform. These feedbacks can create "firehose channels" which quickly transport materials downstream, promoting longitudinal connectivity at the cost of lateral and vertical connectivity (Schumm, Harvey, and Watson 1984; Simon and Hupp 1987; Walter and Merritts 2008; Cluer and Thorne 2013; Hogervorst and Powers 2019; Powers, Helstab, and Niezgoda 2019; Gurnell and Downs 2021).

BOX 1 | Rebalancing lateral connectivity in practice—South Fork McKenzie River, USA.

The South Fork McKenzie River (SFMR) floodplain enhancement project is one of an increasing number of projects restoring rivers and their valley floors to a pre-disturbance, Stage Zero condition (Cluer and Thorne 2013). Prior to restoration, this reach of river was heavily incised (up to 4.3 m) and, less than 30% of the historic floodplain was wetted under base flows (K. Meyer 2019). The project aimed to re-establish hydrologic, geomorphic and biological processes and maximize three-dimensional connectivity at base flows, across the entire width of the valley floor (Flitcroft et al. 2022). The SFMR was restored using the Geomorphic Grade Line (GGL) approach, which involved infilling the incised river channel, allowing the river to spread across the valley floor (Powers, Helstab, and Niezgoda 2019). Three thousand pieces of large wood were used to provide short-term complexity and roughness in disturbed areas, until new channel forms and vegetation established (Figure 7).

This imbalance in connectivity has led to globally widespread, persistent problems in riverscapes, including incision and the associated issues of accelerated bank erosion and in-channel sedimentation, extreme flood events, pollution, and excess nutrients. Furthermore, this has resulted in increasingly disconnected water and terrestrial zones and a shrinking of important marginal ecotones (Knox, Morrison, and Wohl 2022). It follows that rebalancing lateral connectivity where appropriate, by reducing the L ➔ W connectivity and increasing W ➔ L connectivity (e.g., full floodplain reconnection, wetland restoration), will at least partly remedy some of these pervasive issues (Figure 6).

Given the importance of lateral connectivity to river function, rebalancing lateral connectivity should be one of the primary goals of river restoration. Rebalancing lateral connectivity

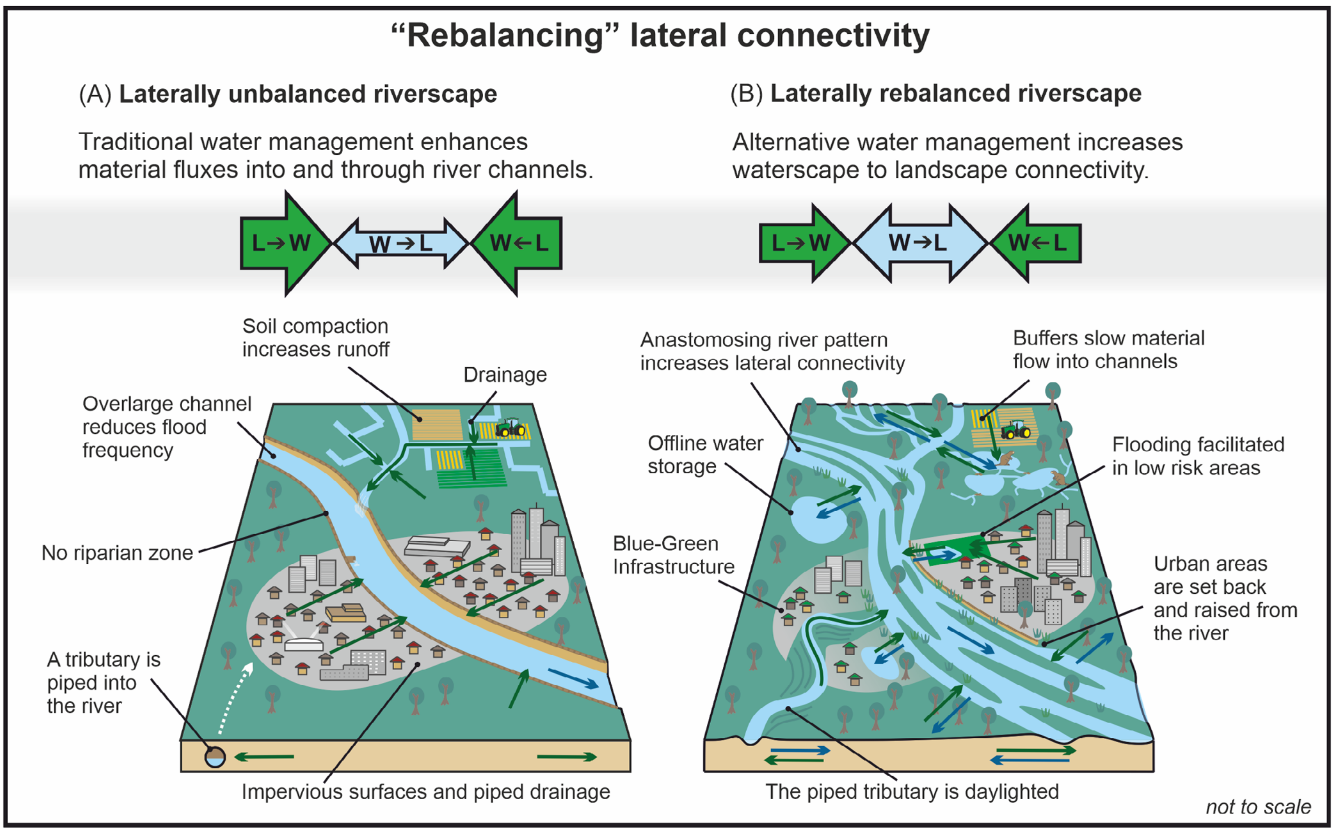

FIGURE 6 | Rebalancing lateral connectivity should be a focus for river management. (A) Traditional river management has reduced fluxes of material out of the waterscape and into the landscape (W ➔ L) while speeding the transport of materials from the landscape into the waterscape (L ➔ W). (B) A "Rebalanced" river reach. Both the landscape and waterscape are managed to slow the flow of materials L ➔ W and (where appropriate) facilitate W ➔ L. Fully rebalancing lateral connectivity is not suitable everywhere, and an evaluation of the pre-disturbance and intended future directions and magnitudes of lateral connectivity is important.

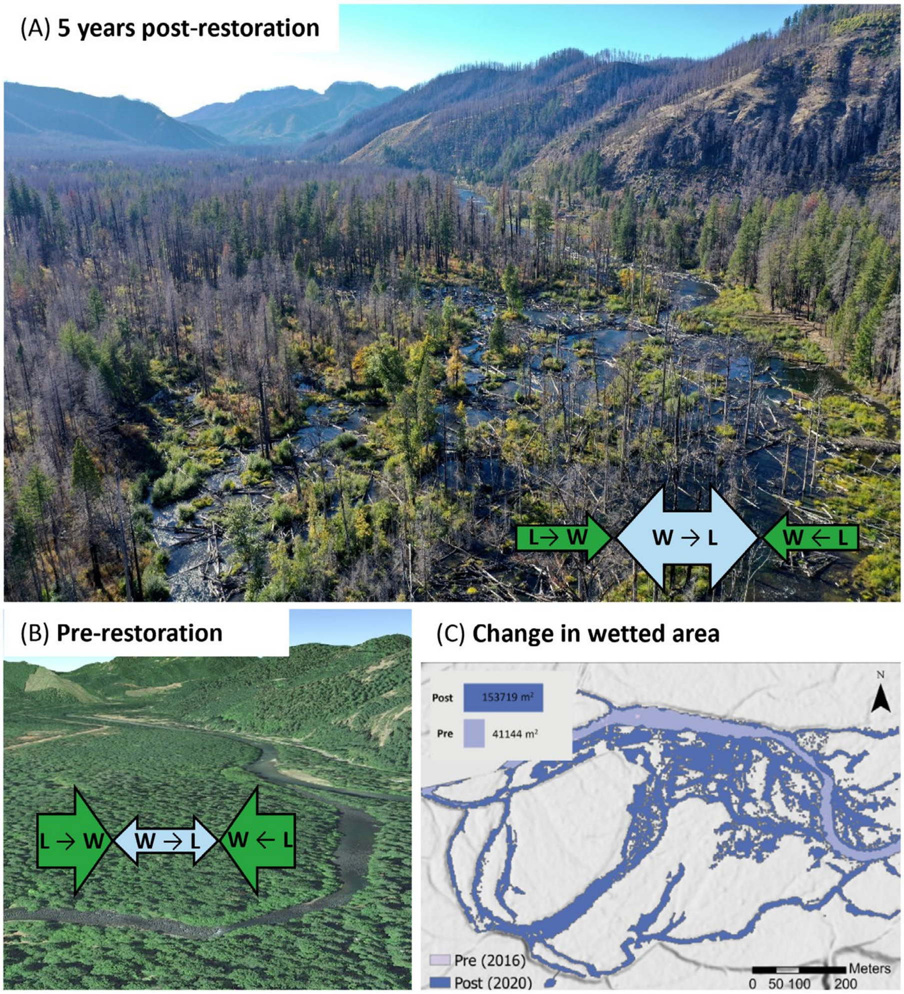

FIGURE 7 | (A) South Fork McKenzie Riverscape post-restoration, (B) pre-restoration, (C) changes in mapped inundation extent during summer, low flow conditions, between pre- and post-restoration surveys. Credit: (A) Kate Meyer, (B) Google Earth, and (C) modified from Flitcroft et al. (2022).

does not mean that we should equalize fluxes L ➔ W and W ➔ L, rather that we should modify the relative balance of these two dimensions to improve the societal services the riverscape provides. Due to centuries of anthropogenic reductions in W ➔ L, increasing these fluxes relative to L ➔ W is usually the aim, particularly in rivers which would have had naturally high levels of W ➔ L. Reducing inputs of water, sediment, nutrients, and pollutants from the terrestrial zone to the channel has long been a goal of river and catchment restoration. For example, buffer strips (Cole, Stockan, and Helliwell 2020), changing land use (Kingsbury-Smith et al. 2023), blue-green urban infrastructure (O'Donnell et al. 2020), and natural flood management (Lane 2017; Quinn et al. 2022) all aim to reduce the speed of L ➔ W connections. More recently, a paradigm shift in river restoration has occurred with an appreciation of the importance of river–floodplain connectivity for both riverscape and landscape health (Beechie et al. 2010; Cluer and Thorne 2013; Wohl 2021). This highlights the importance of W ➔ L connectivity at flow intervals well below bank full discharge (Figure 5).

Although some degree of connectivity is essential to the functioning of river systems, there may not be one "ideal" level of connectivity because the positive and negative effects of connectivity are context dependent. Therefore, identifying a restoration goal for laterally reconnecting processes should consider probable pre-disturbance processes and contemporary opportunities and constraints. A broad idea of historical connectivity can be gained from the landscape context, because not all rivers naturally exhibit high lateral connectivity in both directions (Figure 3). Thus, restoration strategies for lateral connectivity in lowland, low-gradient river corridors will differ to steeper streams with confined valleys. Nevertheless, river long profiles are typically complex and, prior to anthropogenic modification, reaches of high, bidirectional, lateral connectivity would have occurred naturally in many locations due to interruptions in longitudinal connectivity such as geologic constraints, landslides, paraglacial features, log jams, and beaver dams (Wohl, Lininger, and Scott 2018; Mason and Polvi 2023). Key questions remain about where to prioritize the restoration of lateral connectivity within drainage networks. At the catchment scale, heterogeneity in connectivity is key to maximizing ecosystem services and both high and low connectivity are required to ensure the full spectrum of processes and habitats is provided. It is also important to note that some species and habitats may be disadvantaged by increased connectivity, which can increase competition or predation (Bolland et al. 2012; Manfrin et al. 2020).

Understanding which connectivity processes/functions to promote and which processes need management to reduce their negative impacts is key to success but is intrinsically site-specific. Ultimately, the choice of goals and techniques will depend on the catchment and societal contexts, and pragmatic decisions based on the site and permitting considerations. However, techniques to aid riverscape recovery to a more connected state usually involve one or more of the following processes (Figure 6):

1. removal of constraints to lateral processes and connectivity (e.g., levee set-back or removal and channel infilling);
2. increasing channel and floodplain roughness to increase residence times for water, sediment, and organisms and provide opportunity for increased lateral and vertical connectivity;
3. promoting lateral erosion and deposition such as via deflection of water with in-stream structures or increasing overbank flows; and
4. using biology to aid river recovery, such as by introducing beaver, adding large wood, and reducing fluvial power such that plants and animals have sufficient power to modify river processes (Johnson et al. 2019, 2024).

Overall, a common goal of increasing W ➔L connectivity is reducing channel capacity and promoting overbank flows. This may be achieved by re-designing the channel, regrading the valley floor (Powers, Helstab, and Niezgoda 2019), promoting channel aggradation and lateral erosion (e.g., Pollock et al. 2014; J. Wheaton et al. 2019), or increasing channel roughness (e.g., Hankin et al. 2020). While removing obvious constraints to lateral connectivity (e.g., levees) is a crucial goal of restoration, historic incision and channel deepening may still cut off the waterscape from the landscape. Thus, further interventions to kick start bidirectional lateral connectivity may be required.

Anthropogenic constraints have a strong influence on the possibility to restore lateral connecting processes. Complete valley floor reconnection (Box 1) is not possible everywhere. The Dutch Room for Rivers project is an example of restoring lateral connectivity in a constrained setting at a large scale, and was seen as a paradigm shift from fighting against water to living with it (Warner and van Buuren 2011). Room for Rivers involved lowering floodplains, setting back obstacles to floodplain connectivity, adding bypass channels, and increasing water storage within the river corridor (Rijke et al. 2012). This program faced many challenges due to the need to balance restoring connectivity with reducing risks from connectivity. One such challenge has been the post-restoration aggradation of restored side channels, reducing their biodiversity value (Van Denderen et al. 2019) since restoration of structural connectivity was not matched with a restoration of functional connectivity (maintaining flows) and instead may need to be maintained with adaptive management (Stoffers et al. 2022). Furthermore, local residents resisted some of these measures since, despite the aims of the project for nature recovery, the implementation was not seen as "natural" (de Groot and de Groot 2009). Nevertheless, despite the highly managed and controlled nature of the restoration, the Room for Rivers project had broad benefits to biodiversity and flood risk reduction (Klijn, Asselman, and Wagenaar 2018; Verweij, Busscher, and van den Brink 2021; Stoffers et al. 2022).

Biological processes are important in driving and controlling lateral connectivity. For example, organisms may increase in-channel roughness (large wood, vegetation, or beaver dams; Pollock et al. 2014), alter bank stability (e.g., bank protection from riparian vegetation; Tal and Paola 2010), facilitate erosion (e.g., by crayfish; Sanders et al. 2023), and alter catchment drainage and runoff pathways (e.g., riparian buffers, Cole, Stockan, and Helliwell 2020). By laterally reconnecting a channel to the valley floor, unit stream power in river channels may be reduced because river flows are attenuated and stored over areas much larger than that of the channel. This may increase the relative significance of biological processes in affecting riverscape and valley floor forms and dynamics (Johnson et al. 2019; Wohl et al. 2022), as well as lateral connectivity. Therefore, promoting the role of nature's river restorers in the sustainable management of river functioning is a key benefit of rebalancing lateral connectivity. Ultimately, successful rebalancing of lateral connectivity requires consideration of all fluxes, not just water and sediment but also how chemicals, organisms and people will connect to, and interact with, the river.

The initial phase of restoration was completed in 2016. During restoration, water table levels rose and the wetted area at base flow increased by 270% (Flitcroft et al. 2022). Channel form transitioned from predominantly single thread to anastomosing. Consequently, the length of the wetted edge (representing the interface between the aquatic and terrestrial zones) increased by 476% (Flitcroft et al. 2022). The restored condition exhibits a greater degree of W ➔ L lateral connectivity (Figure 7), and consequently integration between the aquatic and terrestrial zones as well as providing a more diverse range of habitats (Hinshaw et al. 2022), and supporting diverse ecosystem services (Flitcroft et al. 2022; Pugh et al. 2022; Hinshaw and Wohl 2023; Jennings et al. 2023).

6 | Conclusions

Anthropogenic modification of the balance of lateral connectivity into and out of watercourses is perhaps the greatest impact of humankind on river systems (Morrison et al. 2023; Rajib et al. 2023). However, anthropogenic impacts on lateral connectivity (e.g., channelization, levees) tend to be less visible than longitudinal obstructions (e.g., dams) and, consequently, less well recognized. A critically required paradigm shift is occurring in river research and management toward enhanced recognition of the importance of laterally connecting processes. This focus marks a shift from conceptualizing rivers primarily as linear features transporting water, matter, and organisms from source to sea, to a network that is intimately integrated with riparian and terrestrial processes, in which lateral exchanges of matter, energy and organisms are as important as longitudinal transport. However, variability in the definition of lateral connectivity and a lack of understanding of how to identify and quantify lateral processes in practice, currently restrict research on, and application of, the concept. Through reviewing work on lateral connectivity across disciplines, we lay the foundation for a broader appreciation of the many components of lateral connectivity in riverscapes. As such, we conclude:

1. Lateral connectivity is defined as the bidirectional transfer of matter, energy and organisms within and between waterscapes (W) and their adjacent landscapes (L). Conceptualizing rivers as connected, laterally, to floodplains and valley side slopes via bidirectional (L ➔ W and W ➔ L) processes forces us to think outside the channel and visualize the river in terms of a riverscape (or river corridor) with laterally connected zones above and below the surface (sensu Stanford and Ward 1993; Biron et al. 2014; Wohl et al. 2021). We use the term *riverscape* to identify the area including and bidirectionally connected to the waterscape.
2. Although lateral connectivity is in many cases driven by hydrological processes, other materials and organisms may, to varying degrees, move independently. Research in river corridor lateral connectivity has typically focused on specific directions (e.g., L ➔ W or W ➔ L) and materials. Therefore, research which considers bidirectional connectivity and the complex interactions between matter, energy and organisms is key.
3. Both L ➔ W and W ➔ L lateral connectivities have important benefits to society and biodiversity, and although the balance between the two varies spatiotemporally, humans have systematically reduced W ➔ L fluxes and increased L ➔ W creating a broad-scale need to rebalance lateral connectivity.
4. Restoring and rebalancing bidirectional lateral connectivity is increasingly recognized as necessary to maximize river ecosystem services and resilience in a changing climate that features more frequent and persistent hydrological extremes. However, since much of our current understanding is based on in-channel processes, greater research on the interaction between waterscapes and landscapes is required. Furthermore, understanding the causal links between morphological interventions and enhanced ecosystem services requires a better understanding not only of the processes involved, but also the temporal and spatial distributions of the bidirectional, lateral fluxes of matter, energy, and organisms.

Author Contributions

Richard J. Mason: conceptualization (lead), funding acquisition (lead), writing – original draft (lead), writing – review and editing (lead). **Matthew F. Johnson:** conceptualization (supporting), supervision (lead), writing – original draft (supporting), writing – review and editing (supporting). **Ellen Wohl:** conceptualization (supporting), writing – original draft (supporting), writing – review and editing (supporting). **Catherine E. Russell:** conceptualization (equal), writing – original draft (equal), writing – review and editing (equal). **Julian D. Olden:** conceptualization (supporting), writing – original draft (supporting), writing – review and editing (supporting). **Lina E. Polvi:** conceptualization (supporting), funding acquisition (supporting), writing – original draft (supporting), writing – review and editing (supporting). **Stephen P. Rice:** conceptualization (equal), writing – original draft (equal), writing – review and editing (equal). **Matthew J. Hemsworth:** writing – review and editing (supporting). **Ryan A. Sponseller:** conceptualization (supporting), writing – review and editing (supporting). **Colin R. Thorne:** conceptualization (supporting), writing – original draft (supporting), writing – review and editing (supporting).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

Related Wires Articles

Natural flood management

Rivers are social-ecological systems: Time to integrate human dimensions into riverscape ecology and management

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