CHAPTER

8

Multiscale ecological resilience in braided rivers

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Introduction

Natural river systems often maintain persistent and stable ecological communities despite their complex environmental structure and dynamic flow regimes (Lytle and Poff, 2004; Chapter 2). This stable-yet-disturbed paradox reflects a number of mechanisms related to resilience, particularly spatiotemporal environmental heterogeneity (McCluney et al., 2014), which can occur in longitudinal, lateral, vertical and temporal dimensions. A large component of this riverine heterogeneity is dictated by dynamic flooding and drying regimes (Death et al., 2015; Poff et al., 1997; Tockner et al., 2010). Moreover, the hierarchical structuring of habitats, populations, communities, and ecosystems across these networks generates ecological attributes that enable rapid responses to perturbations in an asynchronous manner (Firkowski et al., 2022; Gray and Harding, 2010; Terui et al., 2018). The dendritic structure and flow regimes of riverine systems also dictate the movement and exchange of energy and organisms between different environments (Larsen et al., 2019; Loreau et al., 2003; McCluney et al., 2014; Tonkin et al., 2018). Thus, rivers are inherently part of a connected metasystem (see glossary) network of interacting species and habitats, which, coupled with their dynamic flow regimes, facilitates the evolution of a wide suite of resilience mechanisms (Van Looy et al., 2019).

Despite strong theoretical underpinnings for the role of heterogeneity-promoting resilience (Lamy et al., 2020; McCluney et al., 2014; Poff et al., 2018; Tockner et al., 2010; Chapter 1), the mechanisms driving riverine ecosystem resilience have been difficult to study empirically, remain poorly understood, and have likely been compromised by the modification of rivers worldwide. For example, floodplains are particularly important lateral components of river systems, yet are some of the most human-altered riverine habitats (Arscott et al., 2002; Hauer et al., 2016; Peipoch et al., 2015; Tockner and Stanford, 2002, Chapters 3, 5 and 12). This alteration potentially threatens various mechanisms conferring ecological resilience. Thus, although rivers may appear highly resilient to natural dynamism, we need to better understand the drivers of resilience to manage increasing human pressures.

Braided rivers are prime examples of systems that are highly heterogeneous in longitudinal, lateral, vertical and temporal dimensions (Tockner et al., 2006). These rivers form where steep river gradients combine with flashy flows, an abundant supply of bedload-calibre material, and erodible banks to create extensive gravel-based floodplains and braidplains (Box 8.1). Although rare worldwide (Tockner et al., 2003; Tockner and Stanford, 2002), they are ideal for investigating the resilience mechanisms maintaining complex riverine landscapes and their biodiversity and functions. Braided rivers are also an ecological nexus of wider mountain landscapes, sustaining not only aquatic biodiversity but considerable terrestrial biodiversity in connected habitats forming a greater 'meta-ecosystem' (Hauer et al., 2016). Persistence of ecological structure and function in these wider landscapes largely depends on the maintenance of emergent properties such as the consistent (i.e., 'stable') delivery of resources and primary productivity despite regular disturbances (Death et al., 2015; Firkowski et al., 2022). Multiscale biophysical resilience mechanisms are likely integral to this stability of (meta-)populations, (meta-)communities, and (meta-)ecosystems (see glossary) within braided river landscapes, thereby explaining this apparent disturbance-stability paradox. Here, we review the variety of resilience mechanisms that likely underpin braidplain stability despite their regular disturbance. We discuss how within-channel

BOX 8.1

Braided river geomorphology

The multiscale influences that maintain biodiversity in braided rivers play out on a complex background of hydrological and geomorphological processes that shape a dynamic and complex physical environment (Dollar et al., 2007; Tockner et al., 2010). Braided river systems are dominated by continually changing flow and associated bed movement, with on average 30%–60% of the riverbed renewed on a yearly basis and up to 100% on a 5-year interval (Hauer et al., 2016; Hicks et al., 2021; Malard et al., 2006). The braid system is maintained in areas where there are large amounts of erosion linked with steep mountain-to-sea gradients that mean the river transports large amounts of gravel (Ashmore, 2013; Kasprak et al., 2019). Depending on local conditions, a braidplain can also comprise numerous habitats and flow paths with substantial subsurface connectivity, so stable side or mid-channel springs upwell in areas where groundwater flow is forced to the surface or upwells locally through porous gravels (Arscott et al., 2002; Ashmore, 2013; Hauer et al., 2016). The large diversity of habitats is associated with a variety of temperature gradients within the main braid-belt due to variation in groundwater and surface water sources (Hauer et al., 2016; Gray et al., 2016). Individual habitats such as springs, pools, terrestrial gravel-bar islands, and low-flow networks of channels comprise the surrounding lateral braidplain, while the main braid-belt comprises more swiftly running deeper water (Bellmore et al., 2015; Gray et al., 2016). These habitats are connected across the reach and the whole braidplain by groundwater, with lateral habitats being dependent on groundwater flow (Hauer et al., 2016). Thus, the whole braidplain, with highly interlinked but distinct habitats, is one connected system.

spatiotemporal heterogeneity (landscape heterogeneity and asynchrony) could create system resilience at regional or metasystem (see glossary) levels. We also consider species traits that underpin resilience in these inherently disturbed systems, and how such traits facilitate connectivity within the heterogenous landscape. We adopt Holling (1973) concept of resilience, whereby resilience is characterised by a system's persistence and ability to absorb disturbance while maintaining consistent emergent properties, such as the biological communities associated with habitats across a braidplain created by shifting braided channels.

Links between river landscape heterogeneity and ecological resilience

Environmental complexity and heterogeneity are considered integral components of resilience in ecological systems (McCluney et al., 2014; Wohl, 2018; Chapter 10). For example,

heterogeneity at landscape or whole ecosystem levels means underlying characteristics, such as differences in species composition or asynchronous fluctuations of population or community properties in different patches, could scale up to facilitate system-level resilience through spatial and species-based insurance effects (see glossary). These effects mean that although individual local communities may be unstable or fluctuate through time in response to environmental changes, regional-scale aggregate properties such as total metacommunity abundance or biomass may remain constant due to variation in species composition or between local patches (Firkowski et al., 2022; Lamy et al., 2021; Loreau et al., 2003; Wang and Loreau, 2014). Furthermore, highly heterogenous river landscapes have long been theorised to comprise greater ecological resilience to environmental perturbations such as floods (Hering et al., 2004; McCluney et al., 2014; Reice et al., 1990). McCluney et al. (2014) suggested that multiple reach types associated with environmental heterogeneity in a longitudinally connected network will mitigate flooding impacts, because floods would not disturb the whole river evenly. Within-channel refuges resulting from such heterogeneity enable rapid recolonisation of disturbed patches, leading to riverscape-scale resilience even in the face of regular disturbance.

River landscapes, particularly those in dynamically connected river-floodplain ecosystems like braided rivers, thus offer great potential to examine why and how heterogeneity creates resilient ecosystems (Tockner et al., 2003). The degree of heterogeneity within a river varies with a multitude of factors but largely depends on system hydrogeography related to the dendritic structure connecting reaches longitudinally. However, in braided rivers the multiple intertwined channels mean heterogeneity also occurs laterally through the variety of channel types across a braidplain (Box 8.1, Fig. 8.1). These braided river habitats are structured and connected by physical processes acting on a variety of spatial and temporal scales. The spatial arrangement and connectivity of channels within a braidplain therefore set the stage for movement- and connectivity-reliant resilience. Braided river beds, by forming a continuously changing network of aquatic habitats, are perhaps the most dynamic of all river

FIGURE 8.1   A sample of the heterogenous braidplain of the Cass River, a braided river in Canterbury, New Zealand. This braidplain contains a variety of aquatic environments including a stable groundwater spring (A), an upwelling channel spring (B), backwaters (C), a major braid channel (D), and minor channels (E) connected to the main braid (D) by surface water flow.

environments and are an ideal, albeit challenging, environment for testing and understanding relationships between complexity and connectivity that underpin resilience.

Spatial and temporal heterogeneity in braided rivers

A stable, yet disturbed, river model

Resilience in river systems is tightly linked to the characteristics of disturbance regimes (Lytle and Poff, 2004; Poff et al., 1997; Resh et al., 1988; Townsend, 1989, Chapter 21). The high-frequency of flow-related bed disturbance in braided rivers creates an inherently unstable physical environment, meaning only highly resilient ecological communities can persist (Bellmore et al., 2015; Tockner et al., 2006), hence the paradox of a 'stable yet disturbed' ecosystem (Winterbourn, 1997). To better understand the drivers of this stable-yet-disturbed phenomenon, river ecology studies are shifting from single-channel assessments to evaluations of complex channel networks in parallel with the expansion of metasystem theory (Altermatt, 2013; Datry et al., 2016; Tonkin et al., 2018), with braided rivers presenting an extreme example (Gray et al., 2016; Hauer et al., 2016; Tockner et al., 2006). This expansion of multichannel and multiscale research explicitly recognises that a key driver of resilience relates to the wider spatial context involving connectivity dynamics beyond local patches.

Understanding the disturbance-linked drivers of resilience requires considering the scale of disturbance, including those that can tip ecosystems past ecological thresholds (Dent et al., 2002). For example, small-scale disturbances can remove species and dampen interactions in specific habitats such as main channels (Death et al., 2015; Larsen et al., 2019), but wider system stability is likely maintained through connectivity with other braidplain communities (Lamy et al., 2020; McLeod and Leroux, 2021). On the other hand, large-scale disturbances, such as a decadal-scale flood, could reset a whole braidplain through removal of multiple communities simultaneously thus reducing recolonisation potential (Milner et al., 2018; Tonkin, 2022). Large floods could also synchronise population cycles, thereby reducing resilience to near-future events. Thus, resilience is closely connected to the scale of disturbance and must be carefully considered when investigating resilience drivers.

Frequent but moderate flow variations (and thus bed disturbances) caused by unpredictable rain events are a fundamental physical property of braided rivers. Spatial heterogeneity likely underlies a critical resilience-promoting mechanism to counter these frequent but moderate events. In braided rivers such disturbances continually create differing frequencies of spatial and temporal environmental change because the force of water shifts the gravel bed freely, creating new channels and drying others (Box 8.1). The connections between local environments are also constantly altered by the shifting gravel creating a habitat mosaic that facilitates movement of species, resources and nutrients between significantly different, but juxtaposed, physical environments (Kayler et al., 2019; Thorp et al., 2006; Venarsky et al., 2018). Species that occupy these dynamic environments often also harbour traits that enable rapid recolonisation ability or that enhance propensities to avoid or cope with environmental stress (Poff et al., 2018). Thus, not only is disturbance scale important, so too are the hydrogeological processes by which flooding and drying create and destroy habitat and connectivity, leading to a patchy habitat mosaic that contributes positively to resilience.

At the landscape or riverscape scale, the braided river resilience described above is driven by multiple components of flow fluctuation. Variations in flow event periodicity and magnitude across the braidplain and diverse topography (Box 8.1) also drive physical habitat heterogeneity. Under these conditions smaller floods maintain physical bed configurations even though species distributions may be reorganised, whereas larger floods rework the entire bed, creating new habitats and causing local population extirpations (Death et al., 2015). During flow events, the local effects are also spatially decoupled across the braidplain: faster-flowing, lower-lying channels are disturbed more frequently or more rapidly than lateral channels like side braids, which form in the higher elevation gravel mounds as flow increases (Gray et al., 2016) (Fig. 8.1). These asynchronous flow dynamics between distinct habitats create a gradient of patches within the braidplain over which physical drivers of community structure vary, promoting stability at larger scales (Firkowski et al., 2022; Larsen et al., 2019; Townsend, 1989). These types of flow-driven heterogeneity are characteristic of braided rivers and likely a primary reason why braided rivers are inherently resilient at multiple spatiotemporal scales, as we discuss further below.

Influences of the mosaic of heterogeneity

The topographically varying bed surface and heterogeneous hydrogeomorphological processes in braided rivers create a mosaic of habitats both laterally and longitudinally in varying stages of successional composition (Box 8.1). This 'shifting habitat mosaic' (Arscott et al., 2002) maintains a portfolio of habitats in relatively even quantities despite regular physical flow perturbations that change the configuration of local riverbed environments. Although the whole braidplain can be affected in large-scale flood events, which alter channel configuration through the entrainment and redistribution of sediment (Ashmore, 2013; Death et al., 2015), the relative quantities of habitats typically persist. Arscott et al. (2002) showed that while the spatial configuration of aquatic habitats within a braided river had very high turnover (61%) compared with other rivers after flooding, typical flooding caused little change in braid planform or composition of landscape cover. Similarly, the overall composition of abiotic river features measured by Larsen et al. (2019) changed very little after flooding despite potential widespread changes in configuration. Thus, the relatively 'stable' features of braidplain structure can persist despite significant changes in their configuration and associated disruption to their biotic components.

The various habitats within the heterogeneous braidplain mosaic contribute different species compositions and population sizes to overall braidplain biodiversity (Gray et al., 2006; Gray and Harding, 2007). Thus, braided rivers tend to have high beta diversity despite often low local habitat richness (alpha diversity). Braided river main channels are usually relatively 'depauperate' but can contain a few unique species, whereas springs, pools and long disconnected lateral channels can have higher abundances and contribute substantially to total braidplain biomass and diversity (Gray and Harding, 2009; Karaus et al., 2013). Lateral habitats, including springs in particular, often contribute disproportionately to braidplain-wide beta (variation among patches) and gamma (overall braidplain richness) diversity as a result of their unique assemblages (Gray et al., 2006; Gray and Harding, 2009; Karaus et al., 2013). Thus, ecological resilience of these rivers may be particularly influenced by lateral braidplain

aquatic habitats associated with, but disconnected from main braids, which house an array of species ready to recolonise recently disturbed patches. In this way, flood events that reconfigure the braidplain and maintain the relatively constant proportional distribution of habitats, from disturbed main channels to stable lateral springs, are key contributors to the overall biodiversity and biomass characteristic of this stable-yet-disturbed environment.

Unpredictability, stochasticity and the 'mosaic of disturbance'

The proportionally 'stable' nature of braidplain habitats despite constant physical fluxes from flooding and drying perturbations is a mechanism of ecological resilience in and of itself (Vorste et al., 2016). However, the frequency and severity of flow disturbances on each unique habitat depend on the particular location within the braidplain. Larsen et al. (2019) found that flooding slightly reduced species density and richness in the most connected channels, suggesting disturbance was stronger in these channels than in disconnected lateral habitats. This indicates that not only is there a 'shifting habitat mosaic' as Arscott et al. (2002) identified, but also a 'shifting mosaic of disturbance' where lateral and central environments within the braidplain are affected by disturbance at different rates. Thus, in addition to spatial habitat heterogeneity per se, the mosaic of disturbance leads to different patches being spatially decoupled and asynchronous in their disturbance regimes and responses. This adds yet another dimension of multiscale resilience to maintain braided river metacommunities.

The magnitude of a flow disturbance will influence the spatial coupling of habitats during disturbances. For instance, in small magnitude floods the river-bed configuration is maintained and disturbances will not affect all habitats at the same rate. During these floods local habitat quality can be improved by bed movement within wetted channels resetting habitat conditions and preventing weed, fine sediment, or inedible algal build-up, and interrupting species interactions and community assembly processes (Death et al., 2015; Larsen et al., 2019). Indeed, there is a trade-off between the habitat-enhancing effects of floods and their direct effects on species mortality. In these situations, early colonisers often have fast life cycles but low resistance to flood events, creating a succession of species colonisation after flooding (McMullen et al., 2017). However, as floods increase in magnitude their effects propagate beyond individual channels and into the wider braidplain. Larsen et al. (2019) showed that invertebrate communities across a gradient of lateral habitats converge in their composition during flooding events due to species removal and selection for specialist species, and then diverge again afterwards. This sequence reflects differences in local patch conditions and suggests deterministic community assembly processes become stronger with time after a flood (Larsen et al., 2019).

Spatiotemporal environmental heterogeneity or 'mosaics of disturbance' theoretically promote stability and resilience of metacommunities at aggregate scales through both spatial (asynchrony between local community dynamics Wang and Loreau, 2014) and species (varying species responses to the environments de Mazancourt et al., 2013) insurance effects. These mechanisms will be most pronounced when species have strong environmental preferences across different braidplain habitats so that asynchronous environmental fluctuations increase variety in species composition between habitats. For example, the faster flowing, frequently disturbed main and minor channels are dominated by mobile

species or species with fast life cycles such as mayflies (Ephemeroptera) and midges (Chironomidae). As lesser-disturbed channels recover from prior disturbances, their communities will progressively assemble into those comprising species that are vulnerable to disturbance, such as cased caddisflies (Trichoptera) and snails (Mollusca). These species and spatial insurance mechanisms promote increasing resilience at more aggregated scales in both physical environments (patch to braidplain) and biological organisation (populations to communities to metacommunities). The asynchronous and spatially decoupled way flooding and drying impact the habitat mosaic allow community assembly processes to vary laterally between similar habitat types, with some braidplain areas more recently affected by perturbations such as flood scouring than others. Thus, the braidplain represents a spatially and topographically varying gradient of recovery from disturbance (Fig. 8.2) and creates an environment in which local population and community dynamics remain asynchronous through time, promoting stability at aggregate scales (Wang and Loreau, 2014). Therefore, while individual habitats may appear ecologically unstable due to community variation between stochastic events, the asynchronous and time-varying nature
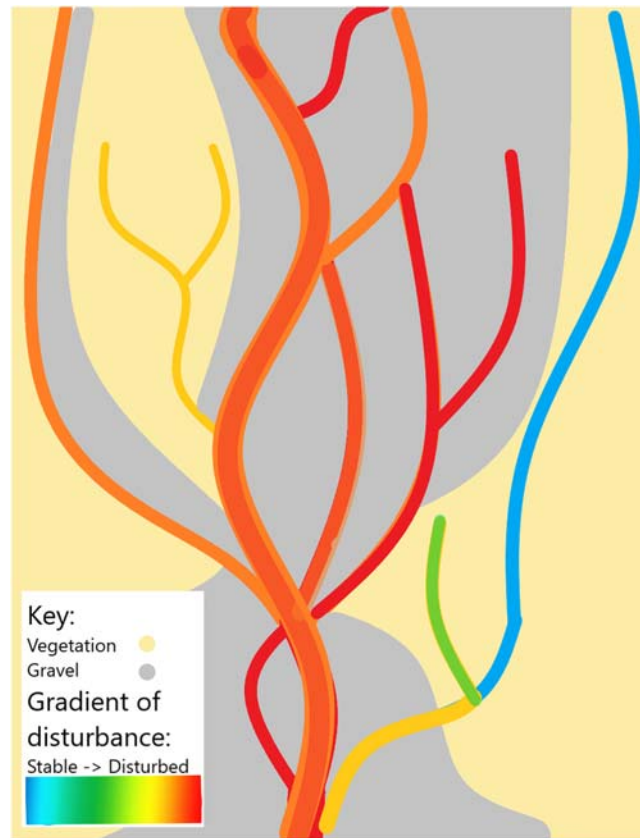

FIGURE 8.2 Mosaic of disturbance that occurs within a braidplain, where central channels are disturbed at more frequent rates of flooding and drying than lateral and more protected channels and upwelling points.

of these perturbations across the braidplain likely enables more stable aggregate biodiversity properties and resilience at larger spatial scales or high levels of biological organisation, although this hypothesis has not been tested.

Disturbance-mediated productivity and interaction strength

Crossed with this gradient of disturbance is variation in the productivity of local habitat conditions and the strength of top-down interactions, which will likely determine the upper limit to species richness and food chain length through combined top-down and bottom-up effects, as well as determining rates of postdisturbance recovery (Chanut et al., 2019; Death and Zimmermann, 2005; McHugh et al., 2010; McIntosh, 2022; Tonkin and Death, 2012). In braided rivers both mid-channel and lateral springs can be high productivity patches, but are subject to differing disturbance regimes associated with flood-driven scour that is an important driver of primary productivity (Biggs, 1995; Snelder et al., 2014). Productivity differences will also vary laterally among major and minor braids, with small shallow channels potentially receiving more solar radiation than larger channels fed by the same water, increasing their productivity but simultaneously rendering them more prone to drying. This creates a mosaic of productivity patch types that further contributes to braidplain heterogeneity. Thus, flow disturbance also dictates food source availability for primary consumers (Dinh and Death, 2018; Snelder et al., 2014) and food web development (McHugh et al., 2010; McIntosh, 2022) in ways that are also stabilising.

Spatiotemporal variation in productivity likely drives the evolution of various dispersal traits among consumers because it means that during certain periods, more disturbed channels, such as minor braids, could also be some of the most productive places for consumers (Bellmore et al., 2015; Dinh and Death, 2018). Consumers in these situations will struggle to track the spatial distribution of resources due to the fast timescales of changes in productivity as small flow changes alter channels and their associated temperature and light regimes. Moreover, by limiting predatory fish presence in disturbed channels (McIntosh, 2022) disturbance probably also creates a mosaic of interaction strengths across the braidplain that likely mean most interaction strengths are weak (Bellmore et al., 2015). The resulting increases in spatial heterogeneity of trophic interactions may serve to dampen overall interaction strength such as predation and enhance aggregate food web stability (Bellmore et al., 2015).

Ecological resilience through continuity and connectivity

Species-specific resilience

Species traits are key to the resilience to environmental fluctuations typical of dynamic braided rivers and rivers more generally (Lytle and Poff, 2004; Poff et al., 2018; Van Looy et al., 2019). Particular traits can facilitate the propagation of resilience from local populations through to community, metacommunity, and meta-ecosystem scales via species interactions and movements facilitated by physical environment connectivity (Jarzyna et al., 2022; Lamy et al., 2020; McLeod and Leroux, 2021). For example, within channels with frequent flow changes and associated flood disturbance, communities tend to be dominated by species

that have fast life cycles and high mobility (Gray and Harding, 2007; Poff et al., 2018). During high flow events, smaller species, or those with burrowing traits, may move into the hyporheic zone and newly created backwaters, allowing rapid recolonisation of the main channel when water recedes (Vorste et al., 2016). Rapid recolonisation, along with spatially decoupled small-scale disturbance events, means that while one channel may appear variable through time, variability of channels at the wider braidplain scale will likely be lower (Bellmore et al., 2015). In fact, there appears to be a trade-off between resistance and resilience of species to flood events whereby smaller, fast-life cycle species may also be subject to greater mortality during floods (i.e., low resistance) but recover faster than resistant species (i.e., high resilience; McMullen et al., 2017).

Resistance and resilience strategies are highly varied among braided river occupants, and associated trait tradeoffs may scale with body size or organismal hierarchy. For instance, high mobility in fish enables movement into flood or temperature refuges as flow or temperature increases (Armstrong et al., 2021; Davey et al., 2006), whereas small-bodied organisms may lose whole cohorts to flood events that are subsequently replaced in the weeks or months following a flood. Such organisms would display staggered life history timings, with bet-hedging strategies likely a common evolutionary adaptation to the unpredictability of flow events in braided rivers (Lytle and Poff, 2004). Higher-level consumers have evolved adaptations to cope with braided river unpredictability: many braided river bird species have the capacity to lay several clutches in a season to combat flooding events that may occur in a breeding season and destroy nests (Heather et al., 2015; Sanders and Maloney, 2002). Furthermore, in years where river channels are scoured by floods many species of river birds can gain alternate food sources from other areas of the braidplain such as ponds and mudflats, despite preferring lipid-rich prey from main channels (Pierce, 1983). Such an array of life history adaptations enables resilience across a variety of spatial, taxonomic and ecological scales (a poorly understood aspect of stability); see (Kéfi et al., 2019), even during very large disturbances during which the whole braidplain may be affected simultaneously.

Movement and metacommunities

So far we have highlighted the strong influence of environmental conditions in structuring communities and driving resilience but as alluded to, populations and communities are also highly connected by movement and water flow (Gray et al., 2016; Richards et al., 2002). Connectivity and movement, when mediated by disturbance, likely play a critical role in system resilience. For example, relatively isolated side tributaries can act as source populations for a range of downstream sink populations (Woodford and McIntosh, 2010). In braided channels there may be more opportunities for various metapopulations and metacommunities, including source-sink dynamics and mass effects (see glossary), to form through the varying levels of connectivity across a patchy habitat. These influences are relatively unstudied at any scale on braidplains. Moreover, a wide range of confluence interactions in a braided riverscape could also create refuges for native fish species, weaken food-web interactions and facilitate population rescue through increased spatial heterogeneity in the same way that side tributary confluences work (Bellmore et al., 2015; Boddy et al., 2019). Finally, patches of groundwater inputs can provide temperature stability and refuges in some areas,

protecting from hot weather and desiccation in the summer and freezing in the winter, and these patches can be seasonally exploited by fish across the braidplain (Caruso, 2006; Hauer et al., 2016; Muhlfeld, 2021). Despite high movement and connectivity, the frequent reconfiguration of the braidplain by disturbance prevents biotic homogenisation of communities (Larsen et al., 2019). Therefore, the connections between distinct river habitats via species movements are vital ingredients in many of the resilience mechanisms we have described. That is, the high connectivity is met by equally high disturbance frequencies to balance its potential negative (i.e. homogenising) effects.

Habitats are not simply connected by species movement, but also by the flow of energy and resources across space, forming meta-ecosystems (Loreau et al., 2003). Resources are carried between aquatic habitat patches by water connectivity, and can move beyond typical ecosystem boundaries such as the land-water interface by the life cycles of aquatic invertebrates, land-water carbon transfer and terrestrial insects washed into the water (Kayler et al., 2019; Larsen et al., 2019; Thorp et al., 2006; Tockner et al., 2006). Braided rivers have extremely high amounts of edge habitat per river kilometre, and this creates tightly interlinked terrestrial and aquatic systems (Tockner et al., 2006). The large edge area likely increases energy exchange and productivity, which can fuel resilience and maintain biomass for both riparian consumers (Paetzold et al., 2005) and instream consumers such as fish (Muhlfeld, 2021). Loss of these edge areas could reduce the overall resources available and resilience of communities. For example, historic alterations such as logging and channelisation that switch rivers from multichannel to single channel typically reduce total edge area and natural features causing reductions in riparian community biomass (Paetzold et al., 2005; Venarsky et al., 2018). Thus, the elevated connectivity associated with the large amount of edge habitat typical of braided channels likely facilitates resilience across a larger spatial environment through species movement and spatial subsidies (Baruch et al., 2021; McLeod and Leroux, 2021; Nyström and Folke, 2001). Braided river connectivity is likely further enhanced due to the multiple flow pathways across the braidplain, frequent flow changes, and high edge-per-river length ratios (Gray et al., 2016; Sambrook Smith et al., 2006; Tockner et al., 2006). Overall, the highly subdivided channels of braided rivers likely mean such connections are especially important for braided river resilience. In particular, they are likely crucial for associated terrestrial consumers like birds that forage in edge habitat.

Biophysical feedbacks, lock-ins and net-negative impact disturbances

The inherently flood-disturbed nature of braided rivers outlined above contributes to ecosystem properties that likely maintain resilience through the constant creation and alteration of habitats, communities, and their reassembly. However, there are many opportunities for these processes to be disrupted and for other disturbance types to be problematic. Floods are only one type of disturbance on a scale of events that drive ecological change with negative or positive impacts (Graham et al., 2021). In river landscapes there are many other forms of disturbance such as invasion, drought, and land acquisition that may negatively impact the net resilience of ecological systems like braided rivers. These types of threats may even drive systems towards thresholds where there is reduced heterogeneity and flow becomes synchronous in a single channel (Fig. 8.3). This in turn is likely to reduce long-term stability of their emergent properties
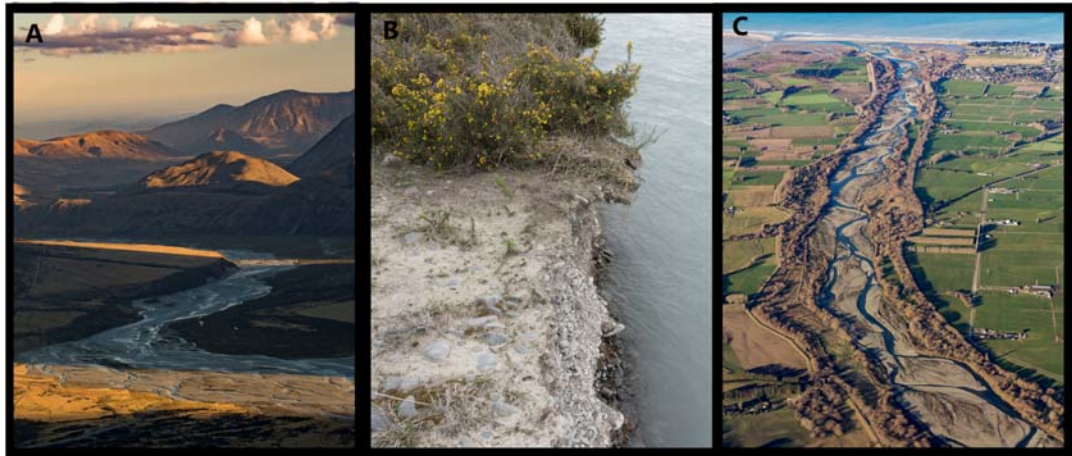
FIGURE 8.3   The Waimakariri river near its start in the Southern Alps runs free (A), but lowland weed and sediment entrapment (B), along with land acquisition and stop banks (artificial levees), can restrict braided river paths (C) causing a loss of heterogeneity and associated inherent resilience.

(Lamy et al., 2020; McCluney et al., 2014), particularly in braided river systems where stability may rely on asynchrony and heterogeneity in the channel network.

Disturbance drivers such as weed invasion or water abstraction, in particular, could disrupt the positive influence of flow-pulse driven disturbances that create resilience, creating biophysical feedback loops that not only impact habitat availability but also reduce the ability of the river system to be resilient to flow disturbances (Gray et al., 2016; Venarsky et al., 2018). Often multiple press disturbances occurring simultaneously will build upon one another in a positive feedback loop that reinforces and facilitates further change (Figs 8.3–8.4).
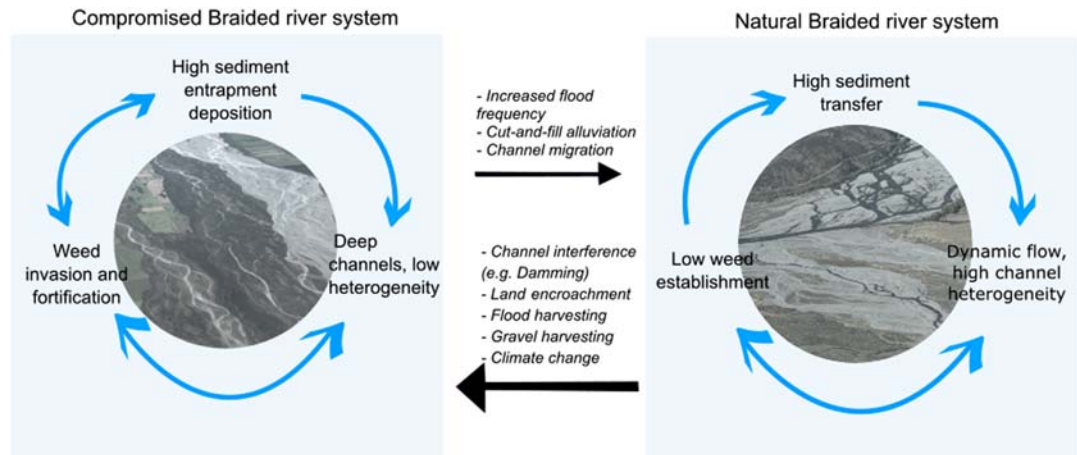

FIGURE 8.4   Press disturbances and anthropomorphic change push ecological properties from one positive feedback loop to an alternative state with different ecosystem properties.

For example, when water is abstracted during floods (flood harvesting), fine sediment and sand particles can build up across the gravel bed through increased deposition (Hicks et al., 2021). This deposition can homogenise many parts of the riverbed through time, often compounded by weedy vegetation that traps more sediment. Vegetation that builds up on gravel bars can then further restrict channel movement and redirect flows to main channels. This increases scour in main channels and further reduces the total number of channels. The weed encroachment creates further sediment entrapment on exposed gravels, reducing the frequency of disturbances and facilitating further weed invasion and channel alteration. Overall, weeds, water abstraction, and sedimentation could combine in a biophysical feedback loop that reduces channel complexity and the inherent resilience that channel heterogeneity provides (Fig. 8.4).

Reduced channel complexity associated with many of these other types of disturbances creates extended periods of lost connectivity between river channels, both longitudinally and laterally, potentially further reducing resilience facilitated by species and resource movements (Larned et al., 2008; Chapter 10). Under this scenario, the flow regime may remain the same but the flow is concentrated into fewer channels due to reduced complexity, increasing potential scour and shear stress on the bed of the main channel environment (Gray et al., 2016). Weed encroachment can also directly cause terrestrial habitat loss and reduce biodiversity of species that have evolved specific traits to deal with the inherently unstable flow regime. For example, the birds that are top predators on braided rivers in New Zealand no longer have areas to nest and feed in weed-dominated areas, whilst simultaneously becoming more vulnerable to nonnative mammalian predators (Maloney et al., 1999; Sanders and Maloney, 2002). Thus, weed invasions push the whole river system towards a much more homogeneous environment where resilience mechanisms inherently associated with a moving bed habitat mosaic are significantly reduced, and the feedbacks likely lock the braidplain in a new degraded and less resilient state.

These biophysical feedbacks and state changes are impacting braided rivers worldwide. In New Zealand, lowland braidplains have frequently been affected by land-use changes, including encroachment and weed invasion (Brummer et al., 2016; MacLeod and Moller, 2006; Monks et al., 2019; Walker et al., 2003), and upland systems are also now being affected by encroachment (Weeks et al., 2013). Thus, it is likely that gradients of press disturbances such as weed invasion and encroachment will affect braided rivers across entire landscapes (Brummer et al., 2016). These situations need to be addressed by management, and comparisons of stability mechanisms between river sites, and between rivers, will help develop solutions. Ecological time-series data and a multidimensional approach to resilience (Donohue et al., 2013; Eagle et al., 2021) will help reveal the combined effects of press and pulse disturbances on these heterogenous systems, and how their resilience may be bolstered in the face of ongoing threats.

Looking forward

Braided rivers are highly heterogeneous systems in both space and time comprising ecological resilience mechanisms that occur at multiple scales. We have laid out a framework

for possible braided river resilience mechanisms, but the interacting disturbances affecting dynamic river systems like braided rivers and the consequences for their resilience remain poorly understood (Graham et al., 2021; Kéfi et al., 2019). In particular, the multiple scales of disturbance that could create a 'mosaic of disturbance' and how the mosaic may influence river ecosystem stability are just beginning to be studied. Large and small floods may have significantly different impacts on the ecological properties of a river (Death et al., 2015), so there is a need to further disentangle their relative effects. The former may increase heterogeneity and asynchrony and the latter may synchronise and destabilise the system across multiple trophic levels. Many potential resilience mechanisms we describe above are driven by the smaller events, but the larger events are critical for maintaining channel morphology and preventing the reduction in river complexity through hydrogeological mechanisms such as the redistribution of sediments. Understanding the relative roles of these different types of disturbance, including their interactions, will be critical as the climate continues to change (Tonkin, 2022). Furthermore, movement of species, matter, and nutrients between the heterogenous environments may have an important effect on ecosystem properties of the wider braidplain given the highly connected system created by disturbance. Thus, understanding how movement contributes to the stability and resilience of food webs and metasystems is an area ripe for further work to create a comprehensive understanding of resilience in spatiotemporally heterogenous systems more generally (Bellmore et al., 2015; McCann et al., 2005; McLeod and Leroux, 2021; Nyström and Folke, 2001). Finally, press disturbances such as gravel and water extraction, channel alteration, invasions, and climate change may primarily have net negative effects on existing mechanisms of river resilience (Figs 8.3—8.4). These types of disturbances provide an opportunity to investigate a gradient of 'scales of disturbance' in braided rivers and identify biophysical feedback loops and thresholds at which inherent mechanisms of resilience are lost. Undertaking such investigations in inherently disturbed systems such as braided rivers will likely reveal ways in which stable ecological properties persist despite drivers of change.

Glossary

Community A group of interacting populations.
Ecosystem A network of interacting species together with their physical environment.
Mass effects Spatial dynamics where there is net flow of individuals between patches.
Meta-ecosystem More than one ecosystem connected by the movement and flow of energy, material, and organisms across distinct physical environmental boundaries (Loreau et al., 2003).
Metacommunity Spatially separated communities connected by dispersal of interacting species (Leibold et al., 2004).
Metapopulation Spatially separated populations connected by dispersal.
Metasystem theory The interaction of local and regional mechanisms that shape populations, communities and ecosystems (Gounand et al., 2018).
Population A group of individuals of the same species that interact.
Source-sink dynamics A dynamic interaction in a metapopulation whereby one population demography allows population growth which allows the excess of individuals to migrate to a second population which would decline to extinction without immigration (Pulliam, 1988).
Species insurance effects A mechanism describing how species vary asynchronously in response to their environment thus regulating aggregate stability among patches (Loreau and de Mazancourt, 2013).
Spatial insurance effects A mechanism whereby asynchronous variation of communities and populations between physical patches allows thus regulating aggregate stability among patches (Wang and Loreau, 2014).

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