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The ecological benefits of more room for rivers

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Christina L. McCabe[1,2,3] ✉, Christoph D. Matthaei[1] & Jonathan D. Tonkin[2,3] ✉

Floodplain river ecosystems have been extensively artificially constrained globally. As climate change heightens flood risks, the command-and-control approach to river flood management is beginning to make way for a paradigm shift towards 'living with water'. The ecological co-benefits of this shift, where rivers are given the space they need to migrate on the landscape, have so far been undervalued. Here we synthesize the ecological benefits of allowing rivers more room to move. We emphasize how the physical and ecological processes of unconfined river channels interact to provide the foundations for ecosystem resilience through spatiotemporal variability in multiple dimensions, including hydrologic and meta-ecosystem connectivity. More informed and sustainable decision-making that involves trade-offs between river ecology and engineering will be aided by elucidating these connections. Giving rivers more room to move can represent a mutually beneficial solution for both the freshwater biodiversity crisis and flood hazard management as climate-driven extremes escalate.

Climate change has forced a rethink of contemporary river-management practices, which were largely built on the presumption of hydroclimatic stationarity[1,2]. The magnitude, frequency and timing of floods and droughts have departed from their historical averages across the globe in recent decades[3–5]. This trend is predicted to continue. Great floods (those exceeding the present 100-year recurrence levels) are expected to recur as often as every two to five years in numerous regions globally[6,7]. Non-stationarity in river flow regimes puts pressure on aging infrastructure and management practices that were designed based on the historical range of variability[1]. Moreover, such alterations to flow regimes can exacerbate the impacts of existing human modifications on river environments[8].

Rivers, floodplains and the connections between them have been modified for centuries to make space for development and, subsequently, to mitigate flood risk. As much as 35% of the human population lives on river floodplains[9], where land conversion and channelization for flood control, navigation or drainage have altered flow and sediment dynamics[10]. This trend has continued in recent decades, with floodplain development nearly doubling in the Yangtze River Economic Belt (China) between 1990 and 2014[11]. Simplified and straightened channels increase the velocity of river flow[12], and disconnection from the floodplain reduces the storage capacity of water and sediment[13], leading to a greater flood risk to downstream environments[14]. Thus, engineering river channels can mitigate flood risk locally, but transfers that risk elsewhere.

As an alternative to the continued re-engineering of flood infrastructure, such as increasing stop bank (levee) height in response to increased flood magnitudes, recent decades have seen a push to widen stop bank boundaries (levee setbacks), giving rivers more room to move on the landscape[15]. Given the economic and social costs of flood disasters, such initiatives are often motivated by the safety of human life and infrastructure. England's 'Making Space for Water' strategy is driven by the economic risk posed by flooding, which has been predicted to increase 20-fold by 2080[16]. Similarly, the Netherlands' 'Room for the River' programme was initiated after floods in 1995 led to the evacuation of over 250,000 people and one million cattle[17]. Although smaller-scale restoration efforts have focused on reconnecting river channels with floodplain waterbodies for ecological purposes

[1]Department of Zoology, University of Otago, Dunedin, New Zealand. [2]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand. [3]Te Pūnaha Matatini Centre of Research Excellence, University of Canterbury, Christchurch, New Zealand. ✉e-mail: christina.mccabe@pg.canterbury.ac.nz; jonathan.tonkin@canterbury.ac.nz

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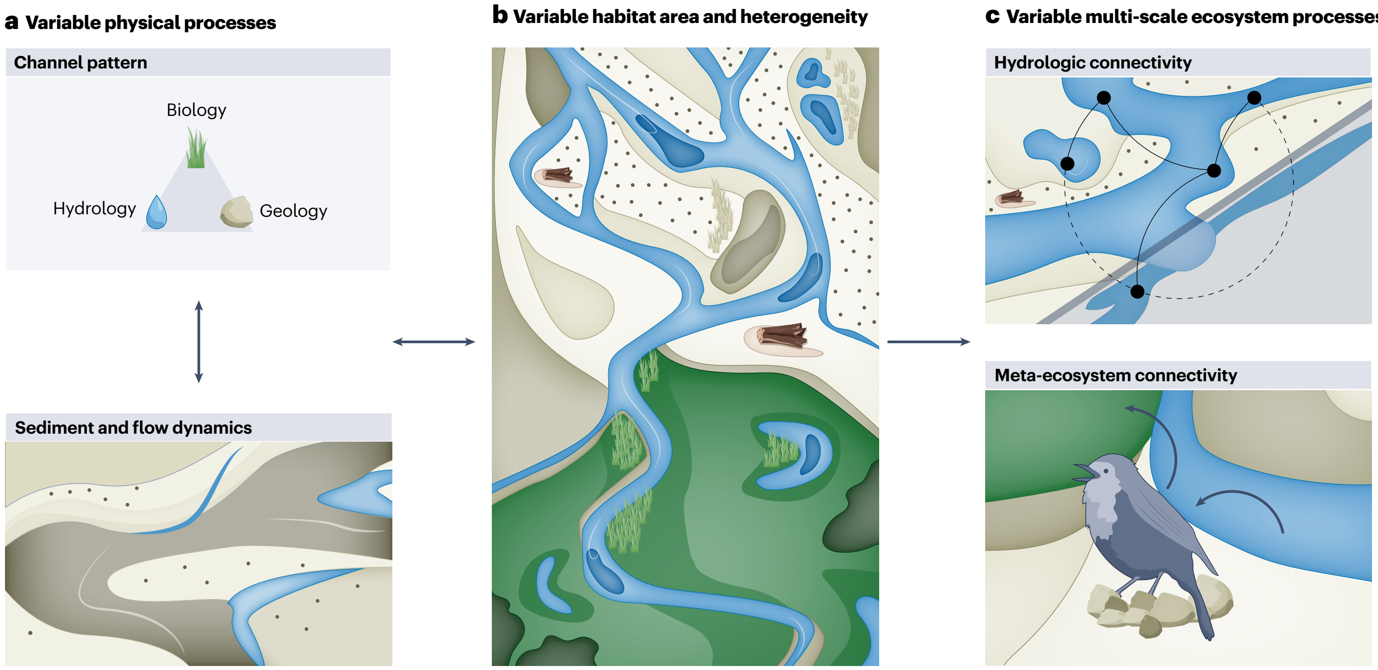

Fig. 1 | The physical and ecological processes of unconfined floodplain river channels interact to provide the foundations for ecosystem resilience. a, The drivers of channel morphology (B, biology; G, geology; H, hydrology[40]) produce a channel pattern unique to local conditions. The resulting channel pattern exists in a positive feedback loop with sediment and flow dynamics. **b**, The physical processes produce habitat that is greater in area and more spatiotemporally heterogeneous than in artificially confined riverscapes. This greater habitat diversity supports greater biological diversity. The habitat and associated biological communities also influence the physical processes, including where vegetation, large wood and ecosystem engineers can influence flow and sediment regimes and the associated channel pattern. **c**, The greater regional biodiversity promoted by a complex habitat mosaic that is in feedback with physical and biological processes supports critical ecosystem processes, including hydrologic connectivity and heterogeneous meta-ecosystems that promote ecosystem resilience.

(see, for example, ref. 18), this paradigm shift to 'living with water' has thus far included limited consideration of ecological outcomes[19,20]. Such initiatives typically remain highly engineered[19] and neglect to comprehensively consider the high degree of spatiotemporal variability in the features and processes that benefit biodiversity in natural floodplain river systems[21,22].

Sustainable river-resource management under hydroclimatic uncertainty requires broadening the scope of considerations to include socially important ecosystem functions[23]. Healthy, functioning rivers provide substantial economic, cultural, aesthetic, scientific and educational contributions to people[24]. However, biodiversity is declining faster in freshwaters than in other environments[25], and habitat degradation, including the constriction of river channels in their floodplains, is a leading cause[26]. Current river-management practices necessarily focus on mitigating flood risk to human populations and infrastructure, whether by increasingly fortifying flood protection infrastructure or giving rivers space to move. In this Review we synthesize the ecological benefits of allowing rivers more room to move. River-management approaches intent on benefitting both people and nature (nature-based solutions[27]) have the potential to provide widespread ecological co-benefits, including the foundations for ecosystem resilience. The physical processes associated with setting back river boundaries have been well documented (for example, in refs. 28–32). Here we focus on the multiscale ecological features and processes that result from complex interactions between the physical processes and habitat dynamism associated with giving rivers room to move. We emphasize three critical benefits: (1) naturally functioning rivers with room to move enable channel patterns to interact with natural flow and sediment regimes; (2) dynamic physical processes enhance habitat diversity; and (3) physical processes and habitat heterogeneity support multiscale ecosystem processes.

River management that works with, rather than against, natural processes is more likely to achieve multifunctional goals (including land drainage, flood protection, conservation and recreation)[32]. First, however, a comprehensive understanding of these features and processes is needed to support more informed and sustainable decision-making involving trade-offs between river ecology and engineering.

Dynamic river features support ecological resilience

Variability is an inherent and essential characteristic of naturally functioning river systems. Fluctuations in water flow, sediment dynamics, temperature and ecological community composition reflect the ever-changing nature of riverscapes. Underpinning these dynamic landscapes are variable physical processes, with the channel pattern interacting with the natural flow and sediment regimes (Fig. 1a). A dynamic equilibrium of active fluvial processes (physical integrity[33]) influences the habitat area and complexity, expanding and contracting with water volume in unconstrained rivers (Fig. 1b), and allowing critical ecosystem functions to take place both within the margins of the main river channel(s)[34] and on connected floodplains[35] (Fig. 1c). Such variability in the river footprint bolsters the resilience of these ecosystems by providing the resources, refuges and environmental heterogeneity that underpin adaptations and responses to disturbance[36].

Channel patterns interact with flow and sediment regimes

The physical riverscape, created by abiotic processes such as flow and sediment dynamics and sometimes biological feedbacks, provides the critical stage on which ecological processes arise[37]. A floodplain river with room to move produces a channel pattern that reflects a dynamic equilibrium between the natural drivers of morphology, spatiotemporally heterogeneous flow disturbances, and connectivity between

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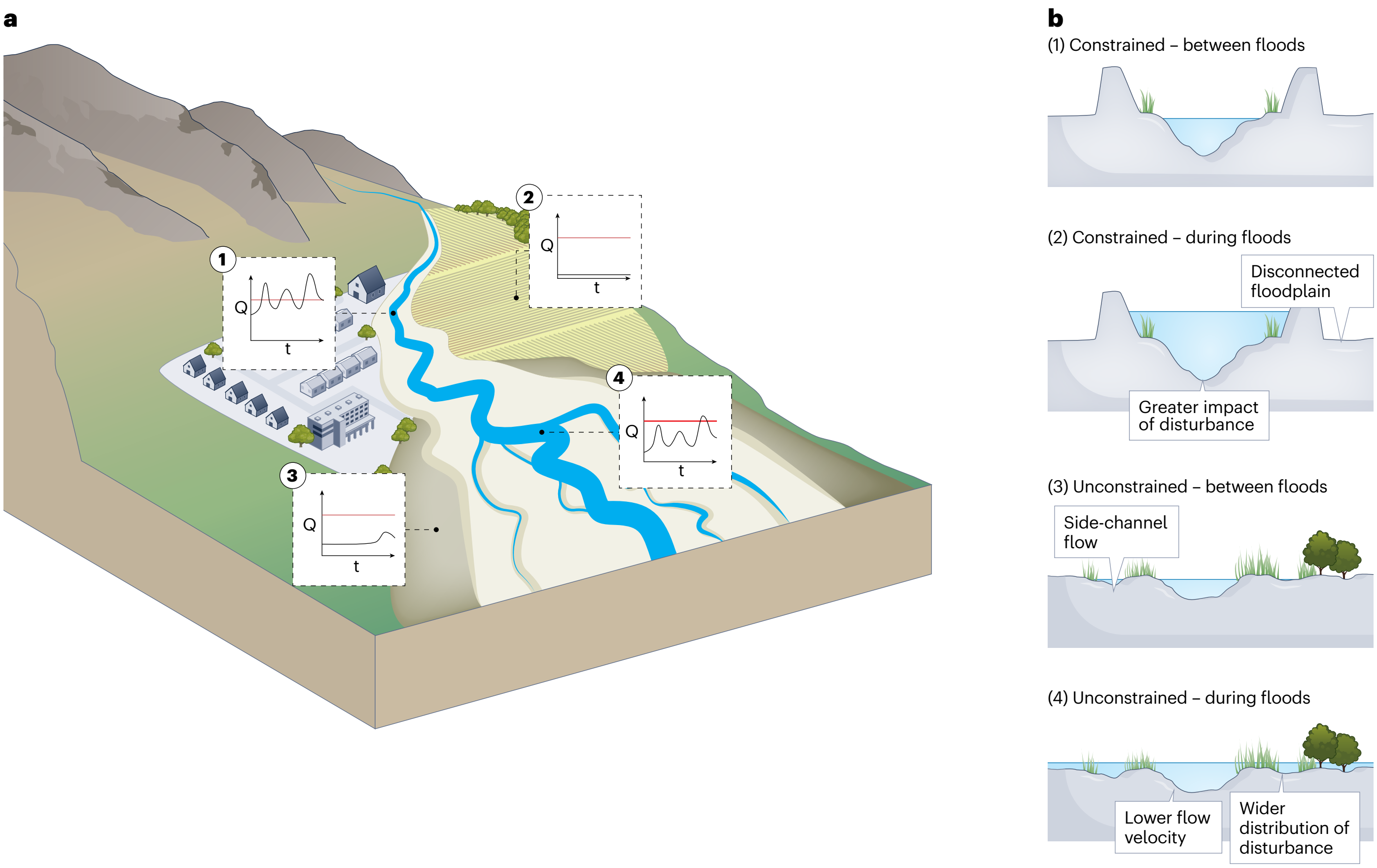

Fig. 2 | When a river has space to move on its floodplain, the natural flow regime (including the magnitude, frequency and temporal dimension) can be expressed in all parts of the riverscape, including within floodplain habitats. **a**, Schematic map outlining discharge *Q* through time *t*: (1) in an artificially confined main channel; (2) on a disconnected floodplain; (3) on a free-flowing floodplain; and (4) in a free-flowing main channel. This schematic highlights both the greater magnitude of flood disturbances in main channels and the lack of natural flow dynamics on disconnected floodplains where riverscapes are unnaturally confined. **b**, A conceptual representation of the cross-section of a main river channel (1) between floods where it is unnaturally constrained; (2) during floods where it is unnaturally constrained; (3) between floods where it is free-flowing; and (4) during floods where it is free-flowing. Here, the magnitude (and thus, impact) of river flow is unnatural in both the confined channel and its disconnected floodplain. By contrast, the unconstrained river system has variation, including side-channel flow between floods and a greater distribution of disturbance magnitude during floods.

sediment source-, transport-, and storage-zones. Such features of the physical riverscape heavily influence the ecological processes underpinning ecosystem resilience.

Drivers of channel morphology underpin physical integrity. The amount rivers naturally move on the landscape depends on the relative influences of the geological, hydrological and biological drivers that shape channel morphology (Fig. 1a). Adjustments between these variable drivers influence the physical integrity of the river: the dynamic equilibrium of fluvial processes, landforms, sediments, and overall river pattern or arrangement[33,38,39]. The natural force imposed by geology in the form of cohesive rock can be imitated by engineered structures[40] and is restored when barriers are removed. Similarly, the influence of hydrological forces in shaping channel morphology is more reflective of the natural flow regime in unconfined floodplain river segments, evading unnatural incision and downstream erosion[21].

Channel morphology interacts with flow and sediment dynamics. Interactions between streamflow and the complex channel morphology of unconstrained rivers create highly dynamic flow disturbances, which are modified in channelized rivers[41]. Where a river has room to move, the volume of water in the main channel is reduced during flood events[42], but supplemented in other important areas, such as secondary channels or floodplain ponds. Groundwater levels and subsurface water storage potential are also increased[42], representing a substantial expansion of groundwater and hyporheic habitats, and can play a significant role in flood attenuation in downstream environments[21]. Thus, allowing rivers to access floodplains is critical to the expression of natural flow regimes, including within floodplain habitats (Fig. 2).

Where a river is unconstrained on its floodplain, sediment source-, transport- and storage-zones can be connected, supporting the natural sediment regime in the catchment. Sediment inputs to a river basin can originate from a disproportionately small area or be delivered within a short period. For example, more than 80% of sediment input to the Amazon River basin originates from the Peruvian and Bolivian Andes, which account for just 10% of the catchment area[43]. These inputs can be transported through the system in places where the main river channel can migrate and connect with fluvial fans, talus, gullies, tributary streams, and other geomorphological features. Although these dynamics can be associated with the flow regime, they operate on different temporal and spatial scales to patterns of flow disturbance and can be less predictable[43]. For instance, increases of inorganic deposited fine sediment have been associated with prolonged stable flow conditions in New Zealand streams[44]. Lateral movement of the river channel on its floodplain also allows for sediment deposition (storage), particularly where a complex channel pattern creates variations in stream power, and thus sediment-carrying capacity, across the riverscape. Spatiotemporal variability in these sediment supply, transport and storage

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b

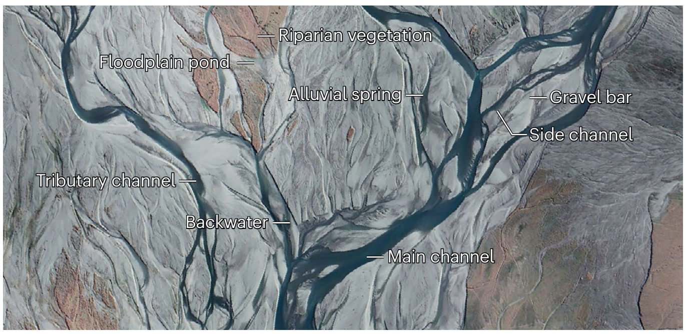

Fig. 3 | Unconstrained rivers contain an extensive variety of habitats, which can each support unique species, life histories and food webs. a,**b**, Both meandering rivers (**a**) and gravel-bed braided rivers (**b**) comprise a high diversity of habitats when left unconstrained, with examples highlighted. The presence and distribution of these types of features depend on riverscape characteristics, including vegetation, geology and hydrology, which influence the channel planform. Credit: background satellite images, **a**, Google, © 2024 Airbus; **b**, Google, © 2024 Maxar Technologies.

processes contributes to the ecologically important habitat diversity in a floodplain river environment.

Dynamic physical processes enhance habitat diversity

The variable physical processes that are promoted in a river with space to move create larger and more complex habitat conditions. Such habitat areas and heterogeneity provide the resources, including food and refuge from disturbance, for biological diversity to thrive at multiple spatial and temporal scales. This diversity spans from genetic diversity within and between species populations to regional species diversity (gamma diversity), as well as variation in ecological communities[45] (beta diversity) and food webs[46]. Moreover, this evolution of habitat diversity can feed back to reinstate the relative role of biological drivers in shaping channel morphology (Fig. 1a).

The habitat and ecological benefits of physical dynamism. Natural sediment and flow dynamics in unmodified rivers influence the expansion and contraction of the ecosystem[34,47] and maintain diversity in the physical landscape[48]. The physical features of unconstrained rivers include side channels, floodplain ponds, gravel bars, backwaters and ephemeral channels (Fig. 3). Thus, habitat diversity can be restored by rewidening river margins. For instance, following restoration of a previously confined river in Scotland, including the removal of bank protection, a 500-m reach of river exhibited a 23% increase in geomorphic features (environmental heterogeneity) and a further 6% increase two years later[48].

Spatiotemporal physical diversity promotes variation in community structure and ecosystem function at multiple spatiotemporal scales[49–52]. This physical variability can include longitudinal diversity in river channel patterns, such as a straight reach followed by a braided reach[51,52] (Fig. 4). Unconstrained floodplain segments can retain more organic matter, water, nutrients and biomass compared to confined river segments[53], and are more productive than wholly aquatic or terrestrial environments[54]. By contrast, although topographically confined reaches can receive greater inputs of allochthonous material, the lower retention capacity of confined channels limits the processing and uptake of such material into aquatic food webs[55]. As a result, naturally confined reaches tend to be places where organic matter is delivered to the system, and floodplain reaches are where it is processed[53] (Fig. 4).

At a finer spatial scale, unique riverine habitats sustain different assemblages of organisms, from distinct invertebrate communities between riffles and pools, to amphibians in floodplain ponds, and mammals frequenting ephemeral habitats[56]. Many organisms need more than one habitat type during their life cycle. For instance, Atlantic salmon (*Salmo salar*) require fast-flowing gravel streambeds for spawning, but calmer channels with protection from predators for fry rearing[57]. Thus, assuming that species track their preferred environmental conditions[50], the more diverse habitats are across riverscapes, the more variable the composition of communities (beta diversity)[58]. For example, active channel spring, floodplain spring, and lateral spring creeks support up to 22 unique invertebrate taxa not found in other aquatic habitats in a New Zealand braided river[59]. This variability in habitat conditions thus increases the total number of species a riverscape can support (gamma diversity)[50,59].

Unconstrained rivers can have a greater occurrence of certain habitat and microhabitat types. Large wood and organic matter accumulations, persisting longer in floodplains than in confined reaches[60,61], increase hydraulic variability, modify in-stream sediment storage[61], and provide carbon and nutrients to floodplain soils[62,63]. Through patterns of scouring and aggradation in freely migrating river channels, wood can be buried deep in the floodplain. Coarse wood, here, can represent an important carbon sink[62], and concentrated sites of decomposition account for up to 99% of energy flow in hyporheic food webs[64]. At the surface, invertebrate assemblages found on driftwood differ considerably from benthic communities[56]. Wetlands and riparian forests also develop and persist where unconstrained rivers create patchy conditions with continually shifting flow and sediment processes[65]. Collectively, these vegetation communities store and slow the flow of water, moderating flood disturbances and replenishing groundwater[66]. Furthermore, the structural complexity provides habitat and resources, including food sources for diverse terrestrial fauna such as birds and small mammals[67].

Natural flow and sediment regimes. Flow disturbances maintain and enhance the quality and quantity of habitats across multiple spatiotemporal scales[68–70]. Smaller but more frequent floods redistribute mineral and organic material, remove decaying matter[71], flush away fine sediments that accumulate in interstitial spaces[21], and deposit fine sediments on surfaces that benefit the recruitment and succession of vegetation[72]. By contrast, more substantial floods that recur relatively infrequently can reorganize the floodplain and are an overriding force that maintains the shifting mosaic of riverine habitats[71,73]. In the Tagliamento River, Italy, large seasonal floods were associated with a turnover of more than 60% of aquatic habitats in a braided floodplain reach and over 20% of habitats in a meandering reach[71]. Such resetting floods[35] can clear all biota and organic material from some habitats, enabling primary succession to restart, and completely remove or rebuild other habitats. Large events of this nature also help to prevent dominant, often invasive, species from overriding communities or engineering the ecosystem towards an alternative stable state[71,74]. The durations of restructuring and regeneration cycles following large-scale perturbations are system-specific. For example, where larger-magnitude floods are associated with certain phases of climatic phenomena, such as the El Niño Southern Oscillation (ENSO), late successional vegetation may

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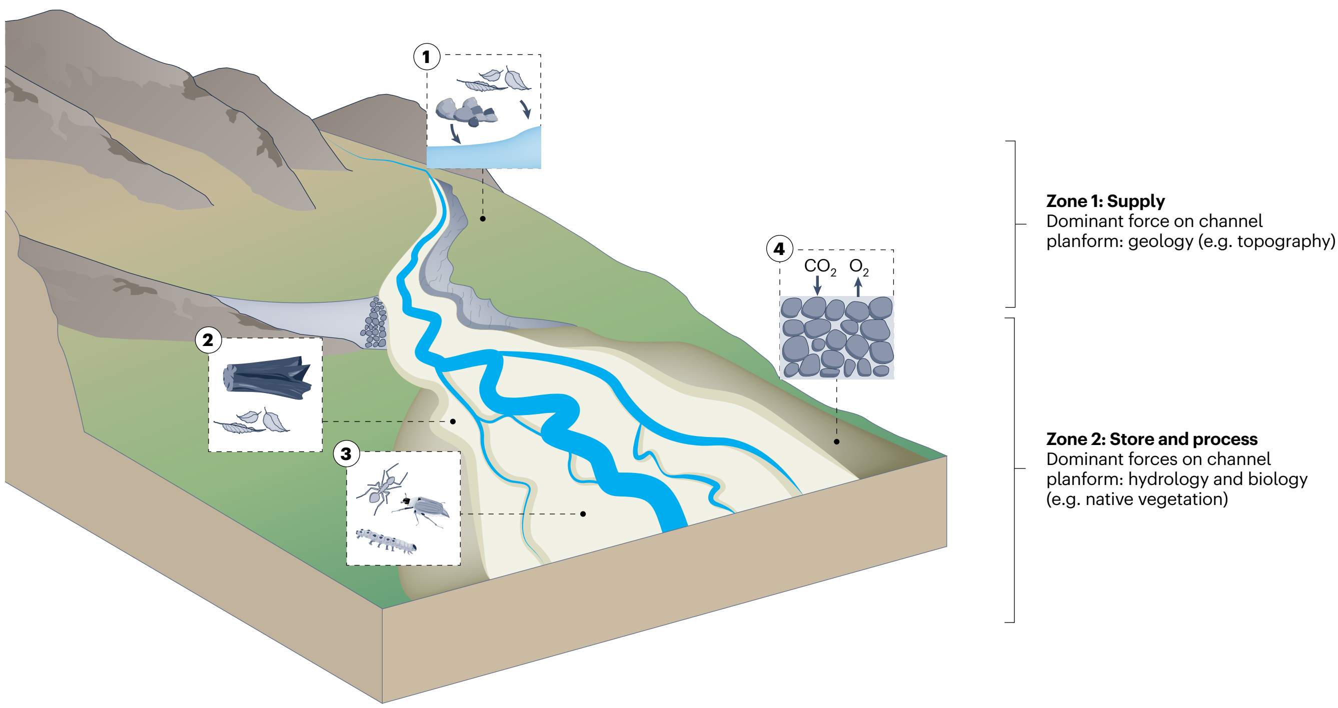

Fig. 4 | A river that is not unnaturally confined will have a planform that varies spatially, producing process domains with contrasting ecosystem functions. The lateral space for channel morphology in zone 1 is strongly influenced by geology, confining the channel. These reaches are likely to have a higher relative supply of sediment and organic matter to the river (1), depending on other local factors including vegetation and topography. Zone 2 is a floodplain segment on a braided river, where hydrological and biological forces will have greater influence than geology on the channel morphology. This reach will store and process more organic matter (2), support greater biodiversity due to greater habitat diversity (3), and be more biogeochemically active, including carbon and nutrient cycling (4).

dominate the floodplain for periods[75]. However, over time, the shifting habitat mosaic maintains an approximately consistent composition of patches at varying stages of succession[75,76], which in turn provides for a greater floodplain biodiversity[49] that may support ecosystem resilience.

A high degree of variability in the flow and sediment regimes—critical to riverine biodiversity and functioning[21,77,78]—meet the ecological requirements for diverse species and biological groups (for example, fish, plants and invertebrates)[79,80]. Organisms in river environments have evolved adaptations (including life history, morphological and/or behavioural) to take advantage of long-term natural rhythms[81,82], including predictable seasonal cycles of flooding and drying in river channels[21,83]. For instance, many fish species need predictable annual floods that occur for up to a week to facilitate spawning[79,84] and stimulate food-web productivity[35], and gammarid amphipods have evolved to synchronize egg-laying with seasonal low flows, thus increasing the survival of young[82]. By contrast, stoneflies have been found to hatch asynchronously as a possible bet-hedging strategy against unpredictable floods[82]. Predictable wet–dry cycling can also promote temporal species diversity, allowing organisms to time-share a particular habitat[85,86]. For instance, Mediterranean-climate streams in northern California cycle between communities of Ephemeroptera, Plecoptera and Trichoptera when pools are connected to the main channel during cooler winter periods, to Odonata, Coleoptera and Heteroptera when disconnected and lentic during summer periods[87].

Variability in riverine sediment conditions also meets the ecological needs of diverse species. Bedload grain-size variation creates diverse habitat, from fine sediment creating the conditions for plant propagules to establish to larger grains creating interstitial spaces that can act as refuges for macroinvertebrates and small fish. These differences can maintain variation in mean body size between fish populations among reaches. For example, substrate grain size can influence river-to-river differences in salmonid fish size and, thus, fecundity[88]. Suspended sediment variation is also important, for example by influencing visibility for predation[43]. For some fish species groups, including salmonids, slightly more turbid water and perceived lower predation risk can increase foraging behaviour[89]. Yet, elevated suspended sediment load typically reduces the ability of visual foragers to obtain food, impacting growth rates, abundance and distribution[89]. Where a river has room to move, the physical processes driving bedload and suspended sediment dynamics are spatiotemporally diverse, supporting distinct resource regimes and organismal life histories across the riverscape[90].

At the community level, the patch dynamics of vegetation are promoted by dynamic disturbance and sediment regimes that create variability in rates of channel migration[91]. For instance, on the cutbank (eroded) side of a channel, higher rates of channel migration can result in species-poor plant communities comprising disturbance specialists, whereas slower rates can increase the structural complexity, density and diversity of plant species[92]. Point bar (depositional) patches, on the other hand, typically follow a classic successional response[92]. Here, short-lived opportunistic vegetation species with year-round reproduction strategies can build propagule pressure rapidly[18] and progressively change environmental conditions (such as ground temperature or soil organic matter content), allowing other species to establish. Naturally functioning meandering rivers therefore allow for a wide range of communities at various stages of succession, ranging from new disturbance-tolerant communities to older and more disturbance-sensitive communities.

Variable physical processes and refuge habitat. In complex and unconstrained riverscapes, disturbances occur with heterogeneous distribution and timing, and varying impacts on habitat types. This heterogeneity increases both the likelihood of refuge habitats existing and their ecological importance (Fig. 5). Disturbed habitats can become

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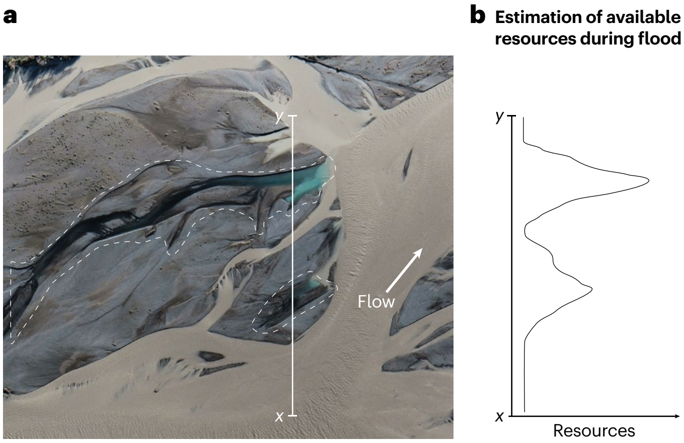

Fig. 5 | Heterogeneous habitats are more likely to include refuges, providing resistance from and resources during disturbances. **a**, Refuges can include mid-channel springs within an active braided-river channel (within the white dashed lines), where less turbid spring water joins the flood waters during a high-flow event. Organisms, including fish and invertebrates, that can access and persist in these springs during a flood will aid recolonization of communities post-disturbance. **b**, A conceptual representation of resource availability along the transect in **a**, where some areas remain available (for example, for food) because the flow disturbance does not affect the whole system to the same degree, simultaneously. Credit: background satellite image in **a**, Google, © 2024 Maxar Technologies.

temporarily unsuitable for certain species, or benefit from increased productivity stimulated by flood pulses[47,93]. Undisturbed habitats provide refuges, offering temporal resistance to disturbances such as floods and droughts[67]. Refuges provide resources including food and spawning habitat, and act as critical reservoirs for the recolonization of communities post-disturbance, thus supporting ecological resilience across the floodplain[91]. Access to such refuges relies on habitat diversity remaining under a range of conditions[36], where some areas are less affected by physical disturbances than others[58]. For instance, when the main channel of an unconstrained river floods, flow may be insufficient to fill and scour secondary channels, or the floodplain may be only partially inundated. By contrast, flooding that occurs in constrained rivers that lack this diversity will impact the entire river bed.

Complex biophysical feedbacks. The relationship between physical and biological processes and habitat area and heterogeneity is bidirectional and includes positive feedback mechanisms. Vegetation can act as a strong biological driver of river geomorphology[94]. In particular, where vegetation growth rates are high and floods less frequent or of smaller magnitudes, vegetated areas can begin to limit the capacity of floods to rework sediments and therefore channel morphology[95,96]. As the dominant control on the landscape shifts towards this biological influence, complex interactions between vegetation, sediment and flow change the river channel pattern[97], and vegetated features such as banks and islands can develop[98]. These landscape features often replace the gravel bars and erodible banks that can be reworked by floods. The fluvial biogeomorphic successional process—a shifting dominance from hydrogeomorphic to ecological processes[99]—can lock the system in an alternative state where hysteresis limits the potential to return to the previous more naturally functioning state[100]. Thus, giving rivers space to move must also consider managing non-native plants in the riparian zone and on the active channel bed that might impair these physical and biological feedbacks.

Biophysical variability aids multiscale ecosystem processes

The physical processes within an unconstrained floodplain river interact with species and communities within the heterogeneous habitat to underpin critical ecosystem processes, including spatiotemporally variable connectivity. Such connectivity can mean the movement of organisms or matter through the system with hydrological flow, as well as meta-ecosystem connectivity involving a reciprocal flux of resources between aquatic and terrestrial systems. This movement of organisms and material through different parts of the system supports the resilience of the ecosystem, as we explain in the following.

Multidimensional hydrologic connectivity. When a river has room to move, the shifting habitat mosaic and expansion and contraction of surface waters maintain the movement of water, organisms, and inorganic and organic materials through the system[22,101]. Hydrologic connectivity is a principal feature of functioning river ecosystems, driven by natural flow regimes and occurring in four dimensions: longitudinal, lateral, vertical and temporal[102,103]. Maintaining diverse connections is important for the movement of individual organisms between habitats for the completion of life-cycle stages, seeking refuge from predators or perturbations, and acquiring resources. Such connectivity is also critical to spatiotemporally connected communities (metacommunities)[104], supporting the movement of resources, gene flow, and recolonization following disturbance. For species to benefit from diverse habitats and resources in the riverscape, they need to be able to access them.

Overbank flows laterally connect floodplain habitats to the main channel. This allows organisms to capitalize on periods of higher productivity on the floodplain, temporarily avoid adverse conditions in the main channel, or access the different habitats required for certain stages of their life cycle[35,47]. For instance, of 85 fish species found in an Amazonian floodplain lake outlet, 20 migrated between the lake and river at different times, likely related to breeding requirements[105]. Some relocated from the lake to the river in August–September when flow was receding, while other species migrated towards the river when flow was rising in December–January[105]. Diverse seasonal migration patterns like this demonstrate the importance of temporally variable connectivity[106].

Restoring the temporal dimension of connectivity between patches enables species with diverse habitat requirements across their life cycle to persist. Fish migrations, for instance, can reflect a range of behaviours and life stages that rely on seasonal connectivity between habitats, including but not limited to spawning, the passive drift of larvae, age-related habitat change, and migrations related to feeding and nutrition[107]. A constrained river thus filters out many species with such requirements.

Vertical continuity between surface water, subsurface water and groundwater is improved by floodplain inundation, which is less available in constrained rivers[42]. During overbank flows, this connectivity enhances the supply of river nutrients vertically within the floodplain and downstream, supporting complex food webs in the hyporheic zone, regulating water temperature[64], and influencing subsurface primary productivity and biogeochemical cycling[42]. The hyporheic zone is a substantial habitat that is up to 60 times wider than the river channel and supports a biomass, including aquatic invertebrates and microbes, that can easily exceed that in the benthos[108]. The hyporheic zone also offers refuge habitats, and many species move in and out of this ecotone regularly[22]. Other organisms occupy the hyporheic zone for their larval stage, including specialized stoneflies that migrate beneath the floodplain up to 2 km away from the river and return to surface waters to emerge two years later[22].

Hydrologic connectivity within a complex habitat mosaic promotes variability in the rates and extents of ecosystem processes[109]. For example, the decomposition of organic matter, such as plant litter, has a controlling influence on nutrient cycling[110]. In some floodplain habitats, decomposition can occur more slowly because abrasion and fragmentation in faster-moving, confined channels accelerate the process[111]. However, other habitats, such as warmer lentic conditions in oxbow lakes, can facilitate faster decomposition via increased

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microbial activity, highlighting the importance of variable habitat conditions across the floodplain. Floodplains are important storage zones for sediments and biogeochemical elements[28,112] that can be redistributed throughout the riverscape during high flows, benefiting the wider meta-ecosystem. For instance, in the floodplains and wetlands of meandering rivers, phosphorus storage can mitigate algal blooms in downstream lakes[13]. The slower-moving water and greater biological productivity of wetland habitats provide more opportunities for nutrients to be incorporated into the ecosystem, rather than being transported downstream. Furthermore, intermittent and ephemeral side channels have more variable nutrient transformations than perennial rivers, greater accumulation and processing of organic matter[113], and more dynamic pulses of respiration and carbon dioxide emissions upon rewetting[114]. Indeed, the rewetting phase in dynamic riverscapes can have widespread implications for biogeochemistry and biodiversity alike[115]. Importantly, both the presence and variability of hydrological connectivity influence the movement of nutrients and matter. This includes slow connections, such as gradual seepage through wetlands, and fast connections, like direct channel flow, each playing a unique role in nutrient cycling and transport.

In multichannel systems such as braided rivers, a dynamic equilibrium exists whereby different patches across the riverscape are connected at different frequencies associated with the magnitude of flooding[116]. Large floods are synchronizing forces (the Moran effect[117]) that connect all habitats in the active channel. Metacommunity structure is shaped by community assembly processes, which are mediated by both spatial habitat mosaics (influencing environmental filtering of which species live there) and temporal asynchrony in connectivity strength between habitat patches (impacting the dispersal of organisms)[116]. This connectivity varies as the habitat mosaic shifts and regenerates over time[118]. For example, in macroinvertebrate communities in floodplain habitats of the Tagliamento River, Italy, floods disrupted the usual species distribution patterns. Instead of species settling in their preferred habitats, flooding caused widespread dispersal, resulting in many organisms ending up in less suitable environments[116]. Thus, in unconstrained rivers, a cyclical process of homogenization can occur during large floods, followed by a divergence in community structure during stable hydrologic periods[116,119].

Meta-ecosystem connectivity. Myriad floodplain habitats provide resources, refuges and reproduction sites for semi-aquatic and terrestrial organisms[54,64,67]. Amphibians, for example, occupy floodplain ponds and wetlands, as well as riparian vegetation, which is critical for providing refuge from fish predation[120]. Many riparian arthropods such as spiders and rove beetles require exposed gravels above the average high-water level for habitat, where they feed on aquatic insects and provide a critical link between aquatic and terrestrial systems[121]. These types of habitat are often the first to be lost in constrained rivers.

The reciprocal flux of material, organisms, and energy between aquatic and terrestrial systems is characteristic of the transitional floodplain environment[122,123]. Terrestrial invertebrates that fall into the river can be a significant prey subsidy for fish, representing up to 50% of annual fish diet and energy budget[124]. Multichannel rivers can comprise extremely high amounts of edge habitats that facilitate reciprocal fluxes between aquatic and terrestrial ecosystems, which is fundamentally important to the resilience of both riparian and in-stream consumers[100]. If food resources become unavailable through the reduction of neighbouring terrestrial habitat, fish can shift their predation to aquatic invertebrates, thus influencing stream food webs[125]. Such foraging across food-web compartments by larger mobile consumers, which is enabled in complex river environments, is a key stabilizing mechanism of food webs[100,126]. One way in which this ecological stability can occur is through the weakened predator–prey interactions that result from coupling of different food-web compartments[127,128]. Furthermore, vast amounts of terrestrial organic carbon are processed in the river, fuelling microbial activity and biogeochemical cycling[123]. These dynamic resource flows from both upstream and lateral terrestrial environments affect the composition of floodplain aquatic communities[122,129]. This flow of resources is reciprocated for terrestrial consumers. Emerging aquatic insects, which can comprise 4–57% of benthic production depending on taxa and local conditions, are a critical food source for birds, bats, amphibians and terrestrial invertebrates[124]. Thus, increasing the available edge area between aquatic and terrestrial systems increases connectivity, including energy exchange, and can contribute to maintaining the biomass in both systems[130,131].

Floodplains are not only important to individual species' habitats and resources, they also provide the arena for critical interactions to occur, affecting both floodplain and upland ecosystems[64]. In the northern Rocky Mountains, Canada, wolves commonly den along floodplain boundaries where they find preferred habitat materials[132]. Floodplains provide a migratory corridor and seasonal resource hotspots for wolf prey, including elk, and are thus the site of important predator–prey interactions[64]. Wolf-killed elk benefit the aquatic ecosystem by providing high nutrient concentrations around the carcass, and wolf predation provides top–down control on elk populations that in turn impacts upland vegetation communities[64].

Some animals migrate considerable distances to access the resources in floodplain environments during certain periods. Each spring, the banded dotterel *Charadrius bicinctus*, an endemic New Zealand bird, travels up to 1,700 km from southeastern Australia to the braided-river floodplains of New Zealand's South Island for breeding[133]. Many other specialist braided-river birds require exposed gravel for egg rearing, where they often create camouflaged nests[134]. Exposed gravel is often first to go when rivers begin to narrow, particularly when invasive vegetation encroaches, threatening at-risk bird species and other gravel-bed specialists[100]. As much as 69% of Europe's breeding area for birds includes wetland habitats, primarily on floodplains, and 82% of bird species in Colorado, United States, rely on riparian vegetation in their reproduction[54]. Many mammals thought of as terrestrial species also use riverine wetlands in stages of their life cycles, including megafauna such as rhinos, bison and elk[64,135]. The high productivity of the floodplain can provide essential resources for winter maintenance of browsers when terrestrial productivity is much lower[64]. Thus, disconnecting rivers from their floodplain habitats not only threatens local species and processes, but also higher-order consumers and predators from neighbouring and larger ecosystems.

Conclusions

As climate change is increasingly impacting flood and drought regimes, and hydroclimatic extremes increase in frequency and magnitude[5,7,136], adapting river-management practices is more pertinent than ever[1,2,137]. Continuing to reinforce flood levees and other structures to mitigate flood risk is increasingly untenable in many situations. The shift from command-and-control to living with water is beginning to take place, but, as we have demonstrated, there are immense ecological co-benefits associated with giving rivers room to move beyond flood control and mitigation. We urge river policy and management to take these co-benefits into account when considering river-management adjustments in an increasingly uncertain world. Floodplain river systems are disproportionately valuable ecosystems, providing 25% of all land-based (that is, not marine) ecosystem services[138], including water retention. There are also opportunities to leverage nature-based and natural climate solutions within riverscape boundaries[27,139]. The distribution and retention of carbon in floodplain soil and large wood deposits impacts global climate, and is regulated by geomorphic processes including channel geometry and hydrological connectivity[140,141].

We emphasize the need to consider the fundamental interactions and resulting ecological processes that can occur where rivers are given more room to move, to aid more sustainable decision-making around trade-offs between river ecology and engineering. Where a

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river is given more space to move, dynamic flow and sediment regimes produce and interact with the channel pattern to create diverse geomorphology; such is the foundation for highly heterogeneous habitats that can support biodiversity at multiple spatiotemporal scales and levels of biological resolution (from genes, to species, to entire food webs). This greater regional biodiversity, in feedback with physical processes, supports critical ecosystem processes including hydrologic connectivity and meta-ecosystem connectivity. Together, the physical and ecological riverscape processes, and interactions between them, underpin the invaluable resilience of these ecosystems.

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Competing interests

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Additional information

Correspondence and requests for materials should be addressed to Christina L. McCabe or Jonathan D. Tonkin.

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