

River beads as a conceptual framework for building carbon storage and resilience to extreme climate events into river management

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Abstract River beads refer to retention zones within a river network that typically occur within wider, lower gradient segments of the river valley. In lowland, floodplain rivers that have been channelized and leveed, beads can also be segments of the river in which engineering has not reduced lateral channel mobility and channel-floodplain connectivity. Decades of channel engineering and flow regulation have reduced the spatial heterogeneity and associated ecosystem functions of beads occurring throughout river networks from headwaters to large, lowland rivers. We discuss the processes that create and maintain spatial heterogeneity within river beads, including examples of beads along mountain streams of the Southern Rockies in which large wood and beaver dams are primary drivers of heterogeneity. We illustrate how spatial heterogeneity of channels and floodplains within beads facilitates storage of organic carbon; retention of water, solutes, sediment, and particulate organic matter; nutrient uptake; biomass and biodiversity; and resilience to disturbance. We conclude by discussing the implications of river beads for understanding solute and particulate organic matter dynamics within river networks and the

implications for river management. We also highlight gaps in current understanding of river form and function related to river beads. River beads provide an example of how geomorphic understanding of river corridor form and process can be used to restore retention and resilience within human-altered river networks.

Keywords River restoration · Organic carbon · Resilience · Extreme climate events · Spatial heterogeneity

Introduction

Traditional river management emphasizes conveyance, uniformity, and stability for navigation and flood control. Conveyance is enhanced through processes such as dredging, channelization, and construction of levees. Uniformity of channel form commonly results from river engineering (Peipoch et al. 2014) and from flow regulation that homogenizes flow and sediment regimes through time and across space (Poff et al. 2007; Wohl et al. 2015). Flow regulation can enhance stability once channel form adjusts to the new flow regime (Ward and Stanford 1995; Shields et al. 2000). Channel stability is also directly enhanced by levees and bank stabilization (e.g., Smith and Winkley 1996). The cumulative result of traditional river management is to create river corridors—which we

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define as including channels and floodplains (Harvey and Gooseff 2015)—that are relatively simple and spatially homogeneous in form and process.

Negative consequences of decades to centuries of traditional river management include high rates of extinction among freshwater organisms (Ricciardi and Rasmussen 1999) and loss of species diversity (Moyle and Mount 2007) eutrophication of freshwaters and nearshore areas (Diaz and Rosenberg 2008) reduced river ecosystem services (Bullock et al. 2011) and loss of organic carbon storage within river corridors (Hanberry et al. 2015; Wohl et al. 2017). In an effort to mitigate these negative consequences, river management is now shifting toward restoring heterogeneity of process and form within river segments and across entire river networks (Brierley and Fryirs 2005, 2016).

Here, we explore organic carbon storage and resiliency through the lens of spatial heterogeneity, with a focus on river beads. Beads, as originally described in Stanford et al. (1996), are wider, lower gradient segments within a river network that are likely to have more spatially extensive floodplains and hyporheic zones than are present along other river segments. Beads were originally described for river networks in high-relief catchments or in rivers with lateral valley confinement. In large, lowland rivers with extensive floodplains, long swaths of river may function as beads. Beads typically have greater retention because of the opportunity to at least temporarily store water, solutes, sediment, and particulate organic matter within the channel, hyporheic zone, and floodplain. Spatially and temporally varying inputs of water, sediment, and—in forested river corridors—large wood, create and maintain spatial heterogeneity to the extent possible for a particular valley geometry, which governs the room available for the channel and floodplain to adjust to varying inputs (Fig. 1).

We examine organic carbon storage in the form of downed, dead wood in the river corridor and floodplain soil organic carbon. We discuss resilience as the ability of physical form and ecological processes in river corridors to resist natural and human-induced disturbances and/or to recover from disturbances, including disturbances associated with extreme climate events (Holling 1973; Webster et al. 1975). Resilient rivers can resist change, recover quickly from change, or both. We use spatial heterogeneity to

describe physically complex channels and floodplains that are the antithesis of highly engineered, uniform and simple river corridors. We use retention to describe storage of water, solutes, particulate organic matter, and mineral sediment over varying time spans. Greater spatial heterogeneity within a river corridor can equate to greater retention because of the presence of surface and subsurface areas of lower flow velocity, lower transport capacity, and greater opportunity for physical storage or biological uptake of materials moving downstream (Schiemer et al. 2001; Battin et al. 2008).

River beads and spatial heterogeneity

Stanford et al. (1996) described river valleys bounded by bedrock as resembling beads on a string when viewed in planform. Beads are wider, lower gradient segments separated by strings of relatively steep, narrow river segments. This pattern of relatively short beads separated by longer strings is common in river networks in high-relief terrain, as illustrated by examples from rivers of diverse size across a spectrum of climatic conditions (Fig. 2a, b). Longitudinal variations in valley geometry that naturally create beads and strings can result from differences in bedrock lithology (Wohl et al. 1994) or the geometry of bedrock joints (Ehlen and Wohl 2002), river response to changes in relative base level (Duvall et al. 2004), or glaciation (Wohl 2013; Hauer et al. 2016). Strings can occur naturally where bedrock outcrops or laterally confined valleys constrain the development of floodplains. Human modifications that transform stretches of river into strings include channelization, levees, and flow regulation, all of which effectively constrict a river to a single, relatively narrow channel.

In large, lowland, alluvial rivers with much broader floodplains, the entire river corridor can function as a bead over lengths of tens to hundreds of kilometers between geologic features that create narrower valley segments along portions of the river's length (Fig. 2c). Spatial heterogeneity also exists within these long beads, in which smaller areas such as floodplain lakes (Lininger and Latrubesse 2016; Sanders et al. 2017) and wetlands (Johnson 2009) or secondary channels and bars (Gurnell et al. 2000) can be particularly retentive. Much of the channel engineering and flow

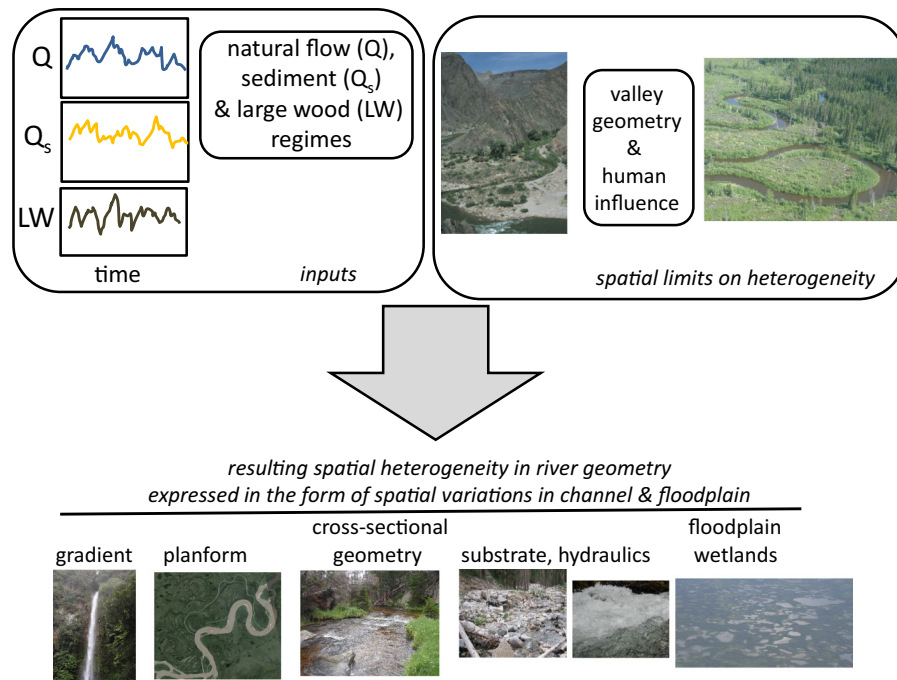


Fig. 1 Schematic illustration of the factors that influence form and process within river beads. Inputs of water, sediment, and, in forested river corridors, large wood, vary across space and through time. These fluctuating inputs interact with the valley geometry to govern river geometry and connectivity within the

river corridor. Valley geometry largely results from geologic controls and geologic history, but anthropogenic modifications such as construction of levees can constrain the effective width of the river corridor within a bead

regulation that we describe in the first paragraphs has essentially changed lowland floodplain rivers from long, nearly continuous beads into a string of smaller beads connected by areas of restricted channel mobility and channel-floodplain connectivity.

Beads in naturally functioning rivers typically have greater lateral channel mobility because of the space available for channel migration. Lateral mobility helps to promote spatial heterogeneity across the river corridor. Lateral migration of the main channel creates cutoff meanders, partly or fully abandoned secondary channels, abandoned and in some cases buried logjams, and floodplain lakes, as well as promoting diversity of grain size, stratigraphy, moisture level, carbon storage, and denitrification rates in floodplain sediments (Collins et al. 2012; Appling et al. 2014) (Fig. 3). Beads can thus be a form of hot spots (McClain et al. 2003) within river networks. River discharges that fluctuate within a natural range of variability help to maintain spatial heterogeneity within river beads because of the importance of peak

flows in transporting sediment and creating channel change and lateral channel mobility (Costa and O'Connor 1995; Friedman and Lee 2002; Kao and Milliman 2008) and the importance of sediment fluxes in maintaining spatially variable patterns of erosion and deposition.

A wider valley bottom and lower channel gradient can also correspond to deposition of sediment, large wood, and particulate organic matter in the channel and on the floodplain. This creates a self-enhancing feedback that promotes spatial heterogeneity (Czuba and Fofoula-Georgiou 2015). Rivers with high sediment loads experience higher annual migration rates (Constantine et al. 2014). Large wood is more likely to accumulate in logjams or wood rafts within beads than in strings (Wohl and Cadot 2011; Livers and Wohl 2016). These logjams obstruct flow; enhance hyporheic exchange flows (Hester and Doyle 2008; Sawyer et al. 2012); create a backwater that traps sediment and coarse particulate organic matter (Beckman and Wohl 2014); promote overbank flow and deposition; enhance the formation of

Fig. 2 Illustrations of strings and beads along rivers of differing size. **a** Biscuit Brook is a small stream in the Catskills Mountains of New York, USA. At left, aerial view (courtesy of Google Earth); ground photos at right and bottom. The floodplain is non-existent in the string portions, but extends to 30–50 m width in the bead portions of the river. **b** North St. Vrain Creek in the Southern Rockies of Colorado, USA. Stream gradient map at upper left illustrates spatial distribution of steep reaches (strings) and lower gradient reaches (beads). Aerial view at right (courtesy of Google Earth), ground photos at lower left. The floodplain is less than twice the width of the active channel in the strings, but can be up to ten times the width of the active channel in the beads. **c** Aerial views of beads (courtesy of Google Earth) and strings along the Yukon River in Alaska, USA. The floodplain is minimal in the strings, but can extend for kilometers in the beads

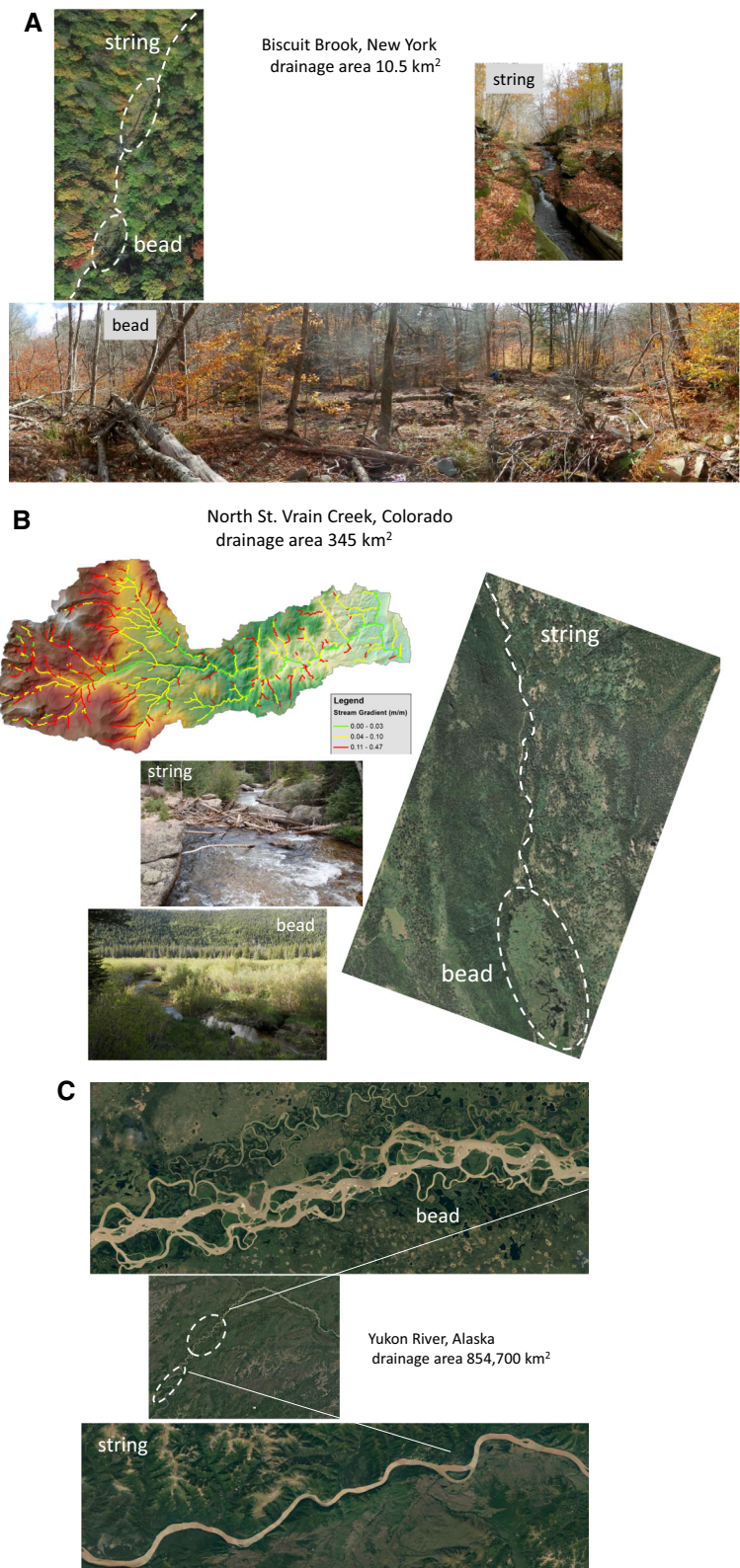
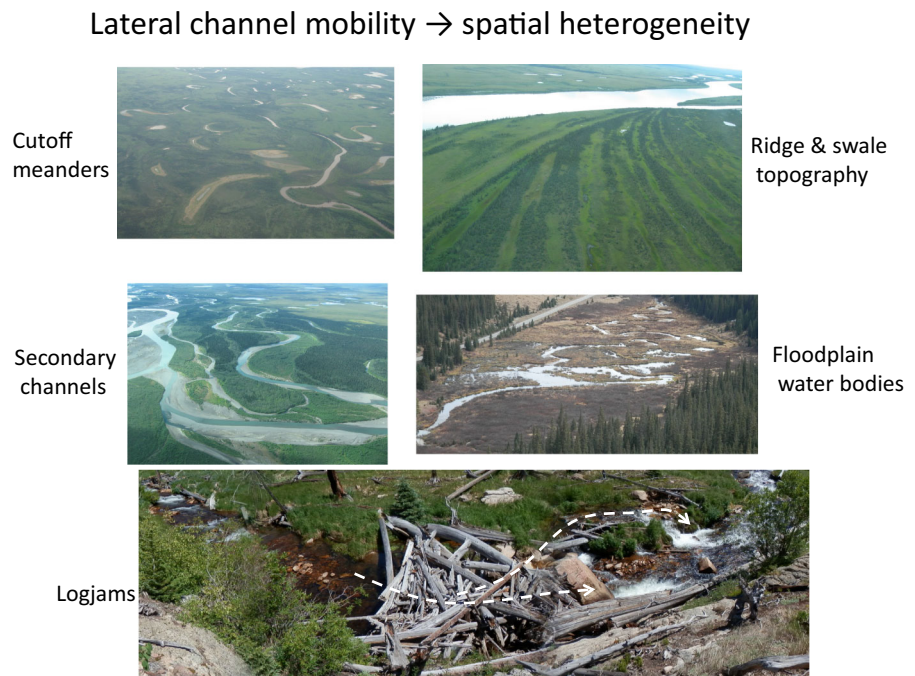


Fig. 3 Examples of spatial heterogeneity resulting from lateral channel mobility at large spatial scales (aerial views of rivers in Alaska, top row and middle row at left; ground view of river in Colorado, middle row at right, with two-lane road at rear of view for scale) to much smaller spatial scales (photo of split flow and gradual channel migration caused by a channel-spanning logjam on a 12-m-wide channel in Colorado, bottom row)



anastomosing channels that branch from the main channel before rejoining the main channel downstream; and ultimately enhance channel-floodplain connectivity and channel-hyporheic connectivity (Triska 1984; Jeffries et al. 2003; Brummer et al. 2006; Fanelli and Lautz 2008; Sear et al. 2010; Wohl 2011; Collins et al. 2012; Sawyer and Cardenas 2012). Conversely, reducing downstream fluxes of water, sediment, and large wood can cause declines in spatial heterogeneity within river beads (Collins and Montgomery 2002; Jacobson et al. 2009).

Case study: river bead form and function in the Southern Rockies

River beads have the potential to be disproportionately important with respect to storage of organic carbon and the resilience of the river ecosystem to disturbances, as illustrated by beads along mountain streams of the Southern Rockies. North St. Vrain Creek (Fig. 2b) exemplifies these streams. The majority of channel length within the river network consists of strings—classic mountain streams that are steep and laterally confined by bedrock valley walls. Quantitative estimates of organic carbon stocks in downed, dead wood, floodplain sediment, and living floodplain

vegetation indicate that beads constitute about 25% of the total channel length within the river network but store about 75% of the organic carbon, primarily in the form of large wood in river beads surrounded by old-growth conifer forest or in the form of saturated, organic-rich sediment in river beads occupied by beavers (*Castor canadensis*) (Wohl et al. 2012). River beads in old-growth forest have significantly greater wood loads (volume of wood per unit area of channel and/or floodplain), greater numbers of channel-spanning logjams, greater backwater pool volume, and larger volumes of coarse particulate organic matter stored within the channel in association with logjams (Wohl and Cadol 2011; Beckman and Wohl 2014; Livers and Wohl 2016; Sutfin 2016).

Beads along North St. Vrain Creek and other rivers in the region have much greater spatial heterogeneity of channel cross-sectional geometry and planform, relative to other segments of the river network, largely as a result of the presence of large wood or beaver dams (Polvi and Wohl 2013; Livers and Wohl 2016). Differences in spatial heterogeneity appear as greater backwater pool volume per unit length of channel, greater standard deviation of channel gradient, and greater ratio of channel length to valley length in beads (Livers and Wohl 2016). These components of spatial heterogeneity equate to greater transient storage of

water, solutes, and particulate organic matter, and to shorter uptake lengths of nitrate (Day 2016). Greater spatial heterogeneity within the channel also equates to greater abundance and diversity of habitat, as reflected in biomass and biodiversity of salmonid fishes (Herdrich 2016) and riparian spiders (Venarsky et al. in revision), both of which prey on the aquatic macroinvertebrates that thrive in these spatially heterogeneous channels. Greater levels of nutrient uptake and biological productivity have also been described for river beads in boreal Canada (Hood and Larson 2014) and in the Northern Rockies (Bellmore and Baxter 2014; Hauer et al. 2016).

Table 1 summarizes results from studies that quantitatively compare various forms of retention and river function within bead and string segments along the same river and compares retention and river function between features characteristic of river beads (e.g., beaver ponds and other floodplain wetlands, gravel bars, secondary channels) and other portions of the river corridor along the same river. The results summarized in this table correspond to broad syntheses such as Newcomer Johnson et al. (2016), which finds that 60% of studies on river restoration involving floodplain reconnection and 75% of studies on restoration with increased wetland surface area report increased nutrient retention.

River beads also can be more resilient to disturbances, as illustrated by the river bead along North St. Vrain Creek that is occupied by a beaver meadow. A beaver meadow is a segment of valley bottom in which beavers have built multiple dams across the channel(s) and floodplain (Polvi and Wohl 2012). At any given time, some of the dams are actively maintained and some are abandoned. Dams and ponds of varying ages and levels of infilling have substrate of different grain sizes and moisture levels and host differing types of vegetation communities (Westbrook et al. 2011), creating a mosaic of floodplain environments that includes secondary channels (John and Klein 2004), dams and berms, and ponds with and without surface hydrologic connectivity to the main channel (Wegener et al. 2017). Because the beaver dams promote overbank flows and hyporheic exchanges, and the secondary channels dug by the beavers help to spread water across the valley bottom, river beads occupied by beavers have high riparian water tables and dense thickets of shrubby willows (*Salix* spp.), river birch (*Betula nigra*), alder (*Alnus* spp.), aspen and

cottonwood (*Populus* spp.), and other deciduous riparian trees and shrubs. High riparian water tables promote resilience to extreme events such as drought (Hood and Bayley 2008) and wildfires, as well as seasonal drying (Albert and Trimble 2000). The multiple dams and ponds and dense riparian vegetation also attenuate peak stream flow (Meentemeyer and Butler 1999; Wegener et al. 2017). An extensive floodplain vegetated with densely growing vegetation promotes resilience to floods, as observed during a September 2013 flood with an estimated recurrence interval exceeding 500 years (Yochum and Moore 2013), which caused minimal erosion and deposition in the North St. Vrain beaver meadow.

The functioning of river beads in the Southern Rockies is strongly influenced by factors that promote spatial heterogeneity and associated retention, connectivity, and resilience. Along North St. Vrain Creek, the primary factors promoting spatial heterogeneity are large wood in river beads within conifer forest and beaver dams and canals in river beads within beaver meadows. For each of these factors, a wide valley bottom of relatively low gradient is a precursor, but the presence of instream obstructions such as large wood or beaver dams is critical to creating a heterogeneous river corridor within that valley bottom.

Figure 4 illustrates how feedbacks can promote or retard spatial heterogeneity within a river bead. For the same valley geometry, two alternate states can exist (Holling 1973; Schröder et al. 2005). When beavers are present (above threshold line in diagram), their dam building maintains a three-dimensional mosaic of active and abandoned ponds and multiple channels in the river corridor. Individual beaver dams create backwater and overbank flow, enhancing channel-floodplain and channel-hyporheic connectivity and maintaining a high riparian water table that supports woody deciduous riparian species favored by beavers for food and dam building. This scenario can persist for thousands of years (Kramer et al. 2012; Polvi and Wohl 2012) and extend for kilometers along river valleys. The river bead is resilient to hydrologic disturbances such as floods, droughts, and wildfire (Westbrook et al. 2006; Hood and Bayley 2008) and highly retentive of water, solutes, particulate organic matter, and sediment (Butler and Malanson 1995; Kramer et al. 2012; Johnston 2014; Wegener et al. 2017). When beavers are removed from a river corridor, their dams fall into disrepair (below

Table 1 Measures of the effects of river beads

(a) Examples of measures of difference between bead and string segments for rivers

Variable ^a	Bead	String	River	Reference
CPOM travel distance (m)	100	237	Salmon River, Idaho	Bellmore and Baxter (2014)
Aquatic invertebrate richness (total no. aq. invert. taxa)	80	51		
Organic carbon storage in river corridor (Mg C/ha)	368	130	N. St. Vrain and Glacier Creeks, CO	Sutfin (2016), Herdrich (2016), Livers and Wohl (2016), Gonzalez (2016)
Salmonid biomass (g/m length of valley)	72.4	39.5		
Number of logjams/100 m channel	5.66	1.54		
Backwater pool volume (m ³ /100 m channel)	32.3	4.3		
Wood load (m ³ wood/100 m valley)	7.4	0.005		
CPOM in backwater pools (m ³ /100 m valley)	45.1	3.8		
Segment export (+) or retention (−) during May–Oct 2015 (kg/10 m)	0.1	2.7	N. St. Vrain Creek, CO	Wegener et al. (2017)
NH ₄ –N	− 0.3	16		
NO ₃ –N	− 1.5	27		
DON	− 1.7	46		
TDN	25	633		
DOC	0.2 × 10 ⁴	1.3 × 10 ⁴		
Water (m ³ /10 m)	0.9	1.01		
Gross primary productivity (g O ₂ /m ² /day)	− 0.72	− 1.77		
Ecosystem respiration (g O ₂ /m ² /day)				

(b) Examples of measures of difference between features characteristic of beads and other segments of channel

Variable	Bead feature	Other	River	Reference
Dissolved inorganic N (g N/m ² /year)	102 ^b	712	Beaver Creek, Quebec, Canada	Naiman and Melillo (1984)
Dissolved organic N	467	3265		
Particulate N	123	861		
Discharge (mm/week)	5.44 ^c	5.61	2nd order watersheds in Maryland Coastal Plain	Correll et al. (2000)
Nitrate (μg N/L)	113	249		

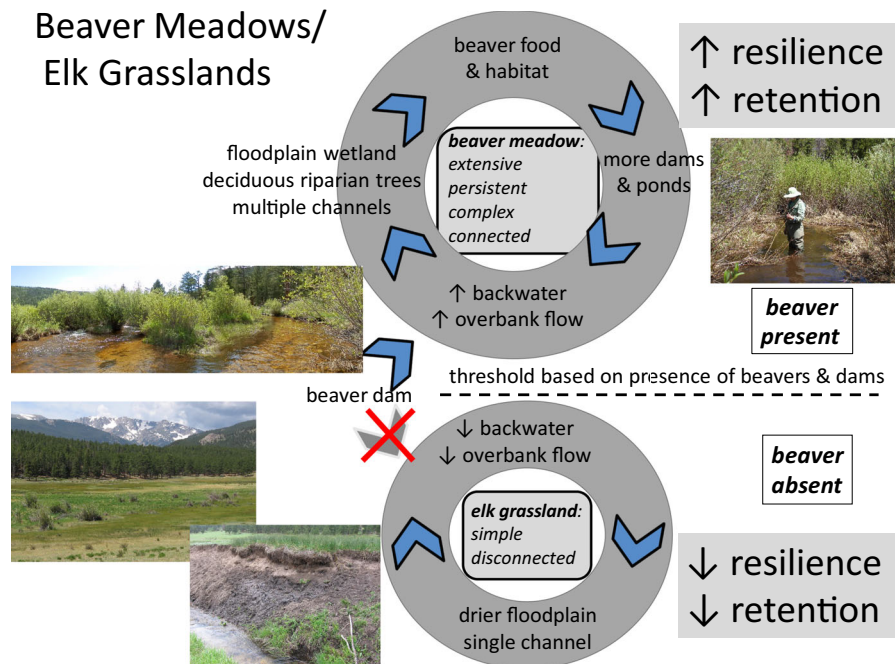
(c) Examples of measures of differences between untreated reaches and reaches restored to function more like river beads

Variable	Restored	Untreated	River	Reference
Denitrification rate (μg N ₂ O-N (g DM) ^{−1} h ^{−1})	1.14 ^d	0.13	Shatto Ditch, Indiana, USA	Roley et al. (2012)
Nitrate-nitrogen (mg N/L)	2.44 ^c	4.32	Olentangy River, Ohio	Mitsch et al. (2005)

Table 1 continued

(c) Examples of measures of differences between untreated reaches and reaches restored to function more like river beads

Variable	Restored	Untreated	River	Reference
Ammonium-N (kg/year)	39.7 ^f	47.8	Store Hansted River, Denmark	Hoffmann et al. (2011)
Nitrate-N (kg/year)	102	1883		
Total N (kg/year)	781	267		
Soluble reactive phosphorus (kg/year)	13.1	28.3		

^aAll values represent medians or averages for populations^bOutput per unit of area for beaver pond versus riffle^c226 ha watershed with beaver pond versus 192 ha watershed without beaver pond^dImplementation of a two-stage ditch with a small, inset floodplain^eComparison of inflow and outflow concentrations in a created wetland^fComparison of inflow and outflow from a restored wet meadow hydrologically reconnected to the river**Fig. 4** Illustration of how feedbacks within river beads promote or limit spatial heterogeneity and resilience of beads. When beavers are present (above threshold line in diagram), their activities maintain a heterogeneous floodplain with wetlands and secondary channels that is laterally and vertically connected to the channel across the entire valley bottom. When

beavers are removed from a river corridor, their dams fall into disrepair, allowing peak flows to remain within the main channel. This channel incises, lowering the riparian water table. Lateral and vertical connectivity within the river corridor and spatial heterogeneity all decline as the valley bottom transforms to a drier environment sometimes referred to as an elk grassland

threshold line in diagram). Peak flows are more likely to remain within the main channel and the greater erosive force of these flows can widen and deepen channels (Green and Westbrook 2009). This causes lowering of the riparian water table and reduces lateral and vertical connectivity within the river corridor.

Where absence of beavers results from intensive grazing by wild ungulates such as elk (*Cervus elaphus*), the drier valley bottom and absence of woody riparian vegetation results in the alternate state of an elk grassland (Wolf et al. 2007). The river bead becomes less resilient to hydrologic disturbances such

as floods and droughts and less retentive of water, solutes, particulate organic matter, and sediment (Wohl 2013). In this example, human activities directly (beaver removal) or indirectly (removal of predators, allowing elk population densities to increase) alter the form and function of the river bead, causing a substantial regime shift in river corridor form and function (Scheffer and Carpenter 2003). The key point of this case study is that, even though valley geometry does not change, the presence of specific features that promote lateral channel movement, backwaters and associated heterogeneity of substrate and hyporheic exchange, and channel-floodplain connectivity are critical to maintaining resilience and retention of the river bead.

The importance of forcing factors such as logjams or beaver dams is not unique to the Southern Rockies. The floodplain-large wood cycle described for rivers of the US Pacific Northwest by Collins et al. (2012), for example, emphasizes the role of abundant large wood and logjams in creating spatial heterogeneity and retention in large, gravel-bed rivers in which logjams create an anastomosing planform. When large wood is no longer present, these channels assume a simpler and more uniform channel and floodplain morphology (Montgomery et al. 1996; Collins and Montgomery 2002), even though valley geometry does not change. Mountain streams of the Southern Rockies also assume a simpler and less retentive form when large wood or beavers are removed (Polvi and Wohl 2013; Wohl and Beckman 2014; Livers and Wohl 2016).

These effects also occur in much larger, lowland rivers. Nineteenth-century removal of the naturally occurring wood raft known as the Great Raft on Louisiana's Red River caused substantial loss of lateral connectivity and spatial heterogeneity of the channel and floodplain (Triska 1984), as well as reductions in overbank deposition (Barrett 1996; Patterson et al. 2003) and presumably in retention and resilience. Larsen et al. (2016) describe how the function of river beads that support pockets of wet monsoon forest within a savannah-dominated landscape in tropical northern Australia can be damaged by river incision that drains the floodplain, but then subsequently restored by bank erosion that recruits large wood to the channel and creates logjams that renew channel-floodplain connectivity and retention.

These examples illustrate how the function of beads as a river form depends entirely on threshold processes that enable heterogeneity and retentiveness. Threshold in this context refers to the transition between alternate states, such as beaver meadows where beaver are present versus elk grasslands where beaver are absent, or anastomosing-channel planform where instream wood loads are sufficiently large and single-channel planform where wood loads are lower (Collins et al. 2012; Wohl and Beckman 2014).

Implications

The function of river beads as segments within a river network that exhibit greater retention of diverse materials and greater resilience to disturbances has at least three important implications. The first involves historical losses or simplification of river beads and our understanding of solute and particulate organic matter dynamics within river networks. The second implication involves river management and restoration that seek to enhance retention and resiliency within river networks. The third implication involves predicting the responses of river networks to extreme climate events based on the characteristics of river beads within the network.

Understanding of solute and particulate organic matter dynamics

As noted earlier, the cumulative effect of centuries of river management has been to greatly simplify and homogenize river corridors. Historical descriptions or photographs of the appearance of river corridors prior to intensive human alteration are more abundant in North America, Australia, and New Zealand than in Eurasia, but sedimentary and fossil records provide indirect information on the form of river corridors around the world prior to changes in land cover and channel geometry (e.g., Brown 2002; Brierley et al. 2005; Hooke 2006; Walter and Merritts 2008; Webb et al. 2014). These diverse lines of evidence indicate that river beads and river networks were much more spatially heterogeneous and retentive in the past both because the processes that create and maintain heterogeneity and retention have been suppressed and because valley geometry has been effectively altered by disconnecting channels from floodplains via

levees and flow regulation. Ecologists estimate that between 200 and 400 million beavers were present in North America prior to commercial fur trapping (Naiman et al. 1988; Butler 1995), for example, compared to populations closer to 15 million at present. Beavers were once equally abundant and widespread in Eurasia (Hartman 1996), but population levels in Europe that dipped close to extinction are now slowly approaching the one million mark (Rosell et al. 2005). Millions of pieces of naturally occurring large wood were removed from rivers throughout the United States (Harmon et al. 1986; Sedell et al. 1991; Wohl 2014) and Europe (Montgomery et al. 2003). Levees and floodplain drainage, channelization and bank stabilization, and flow regulation all reduced the spatial heterogeneity and connectivity within river beads and within river networks as a whole. The net effect of human alterations has been to remove beads from laterally confined rivers that naturally had a bead-string configuration and to create long segments of string along lowland, floodplain rivers that once functioned more as a longitudinally continuous bead.

It is difficult to overemphasize the magnitude and extent of these changes. The earliest written descriptions of rivers in locations as diverse as the southeastern United States (Reuss 2004), the upper Mississippi River basin (Andersen et al. 1996; McMahon and Karamanski 2009), or the Willamette River of Oregon (Sedell and Luchessa 1982), as well as rivers in southeastern Australia (Brierley et al. 2005), clearly indicate that many forested rivers featured closely spaced, almost continuous beads. Stepped beaver ponds, logjam-induced backwaters and anastomosing channels, and other forms of spatial heterogeneity were so abundant that early European explorers regularly complained of the difficulty of following a river channel because of nearly continual obstructions and uncertainties about where the main channel actually lay within a valley. Large, lowland rivers of Europe such as the Rhine or the Danube also historically presented serious challenges to navigation because of their anastomosing planform within alluvial portions of the river corridor (Van den Brink et al. 1996; Pisut 2002).

Even in the absence of riparian forests and beavers, natural river channels in warm desert and grassland environments commonly were more spatially heterogeneous and laterally mobile prior to intensive human alterations of flow regime and channel geometry. On

the US Great Plains, for example, flow regulation caused broad, shallow, highly mobile braided rivers to narrow and become less laterally mobile (Williams 1978; Nadler and Schumm 1981). This resulted in loss of heterogeneity associated with secondary channels and mid-channel bars that provided critical habitat for native fishes and migratory birds, many species of which are now at risk (NRC 2005).

Desert rivers in the mountain or plateau regions of the southwestern US exemplify the string and bead morphology with reaches of narrow canyons between wider, more retentive reaches. The less-confined reaches have predominantly incised, partly as a result of water tables lowered through groundwater extraction and flow regulation, leading to the decline of habitat and native species (Rinne and Minckley 1991). Although large wood is more recognized as a key component of river ecosystems in forested river corridors with wetter climates, Minckley and Rinne (1985) note that large wood can stabilize transitory habitat in hydrologically flashy desert channels and can provide an important source of organic nutrients. The widespread reduction of organic matter inputs to desert streams has likely led to reduced heterogeneity in systems naturally subject to limited nutrient availability and floodplain habitat. Similarly, living trees and large wood in ephemeral rivers of interior Australia promote retention (Graeme and Dunkerley 1993; Jacobson et al. 1999) and spatial heterogeneity (Dunkerley 2008, 2014).

Water and sediment regulation has also caused dramatic changes to the planform of gravel-bed braided rivers, forcing the transition from planforms dominated by braiding to those dominated by long stretches of meandering or otherwise narrower channels (Piégay et al. 2009). Wide, retentive, braided reaches of non-forested rivers historically provided ecosystems with high biodiversity that supported unique species (Tockner et al. 2006). The loss of these braided reaches represents a transition to narrower, more homogenous meandering planforms that lack comparable ecosystem structure, processes, and services (Piégay et al. 2009).

Beads also record signals of landscape change that have altered fluxes of diverse materials along river corridors over varying time spans. Floodplains and deltas retain sediment, in particular, in a manner that provides information about processes occurring upstream (Jacobson and Coleman 1986; Knox 2001).

In networks with abundant strings, beads such as lake deltas can provide unique sources of environmental information by storing relatively long records of sediment and carbon. The function of subalpine lake deltas as beads that store carbon strongly correlates with upstream processes that impact carbon dynamics (Scott and Wohl 2017). This highlights how sensitive beads can be as magnifiers of network-scale nutrient dynamics.

Removal of the sources of spatial heterogeneity within river beads and artificial reductions in the effective width and retention of river beads via alterations such as flow regulation or construction of levees effectively reduced the abundance and function of river beads. These changes have likely caused rivers to behave more as pipes that passively transport material downstream and less as reactors in which materials are processed and stored (Casas-Ruiz et al. 2017). Figure 5a presents a schematic illustration of a river network prior to intensive human alteration of the watershed, whereas Fig. 5b reflects the contemporary appearance of many river networks. The differences in the abundance and function of river beads between

these two illustrations has not been considered in measuring and modeling river processes such as flood attenuation, nutrient dynamics, organic carbon storage, or river resilience. Although the scientific community is aware that certain areas of the landscape such as riparian wetlands can function as nitrogen sinks (Seitzinger et al. 2006; Kellogg et al. 2010), existing models of nutrient dynamics are based on highly simplistic conceptualizations of river networks as uniform, unobstructed channels (no floodplains) with consistent trends in size in relation to increasing discharge (e.g., Wollheim et al. 2006; Raymond et al. 2012). For many river networks that have been intensively altered by humans, these simplifications may not be overly limiting, particularly where actual field measurements of relevant processes have been used to calibrate or validate the model. When assumed to represent natural river networks, however, these simplifications could result in significant misrepresentation of relative rates of uptake of nitrate and other nutrients and significant misperceptions of how river networks can operate. Peter Raymond speculated that his model of gas transfer velocities in rivers (Raymond

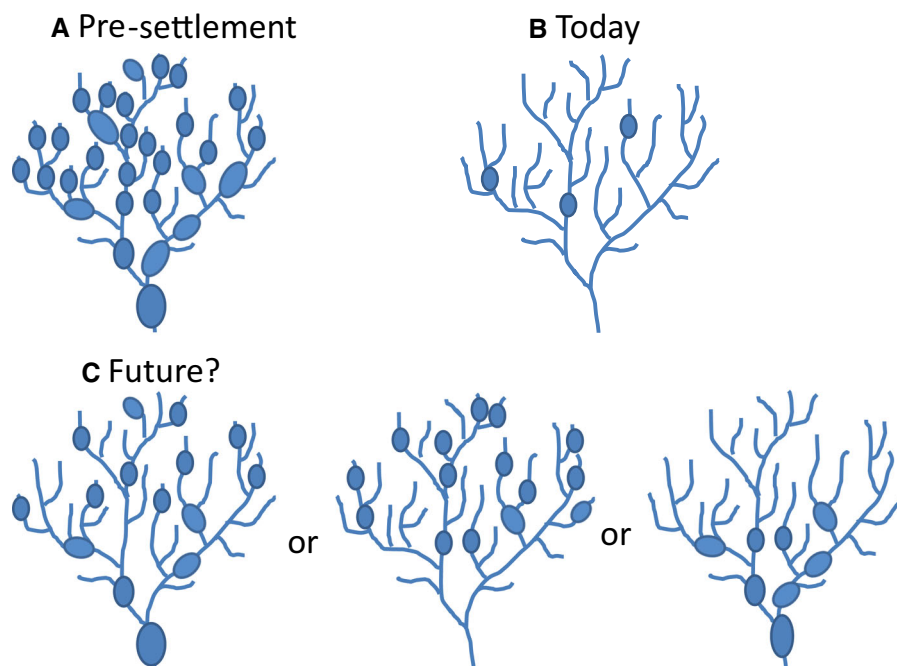


Fig. 5 The abundance of river beads present prior to intensive human alteration of river networks and drainage basins (a) has declined substantially in most managed river networks (b). River management could restore spatial heterogeneity, connectivity, retention, and resilience in at least some of these beads,

but it is not clear whether restoration should target beads distributed throughout the network, beads concentrated in relatively small sub-catchments, or beads along rivers with larger drainage areas (c)

et al. 2012) and other models of network-scale gas emissions might be sensitive to where in a river network the retention features are located (pers. comm. 21 Jan. 2017). Real river networks might also be sensitive to the spatial distribution or size of individual beads, as well as the abundance of beads. Addressing these uncertainties is a research need.

At least one study has considered the effect of historical simplification of a very large river bead on organic carbon storage. Investigating organic carbon stocks in floodplain soil, large wood, and living riparian vegetation, Hanberry et al. (2015) estimated that the lower Mississippi River alluvial corridor, which covers more than 1000 km², now stores only 2% of its historical organic carbon stock. Given that contemporary organic carbon storage of 97 Tg in this area could reasonably be increased to 335 Tg with reforestation of marginal agricultural land (Hanberry et al. 2015), the current emphasis on carbon sequestration through upland afforestation (van der Gaast et al. 2016) should be expanded to explicitly emphasize the carbon sequestration potential of river corridors. In this context, substantial increases in carbon storage could also be achieved with beaver reintroduction (Wohl 2013; Johnston 2014).

River management and restoration

River management that emphasizes the identification, protection, and restoration of river beads is critical to maintaining the vitality of river systems under a changing climate. Identification of river segments that are physically capable of serving as river beads and that are available for management can be used to prioritize sites within a river network for restoration. Figure 6 illustrates examples from an agricultural catchment in Scotland and a gravel-bed river in Italy. In each case, only a small segment of the entire channel length is available for restoration of form and function, but if a sufficient number of beads can be restored in this manner, it might be possible to mitigate the effects of watershed-wide increases in nutrient runoff (Bernhardt and Palmer 2011), for example. Similarly, restoration of numerous beads within a river network could provide substantial attenuation of flood peaks and sustain river base flows during dry periods, given the demonstrated ability of individual river beads to attenuate floods and store and gradually release water during droughts (Albert and Trimble

2000; Westbrook et al. 2006; Hood and Bayley 2008; Wegener et al. 2017). Restoration of function within river beads can also mitigate channel incision and store substantial quantities of the sand-size and finer sediment (Pollock et al. 2014) that are an important pollutant in rivers when present in excess quantities (US EPA 1997).

Predicting river responses to extreme climate events

As retention zones within river networks, river beads illustrate how coupling among physical characteristics, biogeochemical processes, and ecosystem responses within the river corridor can promote resilience to disturbances. Diverse studies indicate that river beads commonly have several characteristics that make them more resilient to disturbances than other portions of the river network. These characteristics include: higher riparian water tables and larger areas of open water that can buffer response to droughts (Westbrook et al. 2006; Hood and Bayley 2008); greater accommodation space for at least temporary storage of water, sediment, and particulate organic matter moving downstream as a result of floods and/or hillslope instability such as landslides (Goodbred and Kuehl 1998; Fryirs et al. 2007); and greater hyporheic exchange flows and more extensive riparian vegetation that can reduce downstream fluxes of solutes, such as pulses of nitrate moving into river networks from agricultural or urban lands during storm runoff (Casey and Klaine 2001; Wegener et al. 2017). Consequently, larger and/or more numerous beads within a river network should equate to greater resilience to hydrologic extremes of flood and drought, as well as greater resilience to other inputs (e.g., sediment, nutrients) resulting from heavy precipitation and storm runoff. As noted in the next section, we do not yet have the ability to quantitatively predict the resilience created by numerous smaller beads versus a few large beads within a river network, but the functions associated with river beads are likely to be critical to protecting river resilience to extreme climate events.

As climate continues to change, the magnitude and frequency of extreme climate events are likely to increase in diverse geographic regions, straining water resource supply systems and the sustainability of freshwater ecosystems (Death et al. 2015). The manner in which river networks and specific segments



Fig. 6 Examples of restoration of bead form and function. **a** Floodplain reconnection along a limited portion of the River Tweed in Scotland, an agricultural catchment in which the river was channelized and floodplain wetlands were drained. Area of reconnected floodplain indicated by white bracket. (Photograph courtesy of Derek Robeson) **b** Removal of grade-control structures (indicated by white arrows along right side of river

in this view) and bank stabilization along a portion of the Mareit River in Italy allowed increased spatial heterogeneity associated with gravel bars, some of which will likely support woody riparian vegetation as the channel continues to adjust following infrastructure removal. (Photograph courtesy of Francesco Comiti)

of rivers respond to extreme events is commonly nonlinear and not necessarily easy to predict or mitigate (Phillips and Van Dyke 2016). Protecting and restoring function within river beads can help to build resilience back into river networks, although fundamental uncertainties remain about how

differences in the spatial distribution and relative size of river beads might influence the cumulative effect of these retention features at network scales (Fig. 5c). These uncertainties can be addressed using a combined approach of field studies, including sustained monitoring of restored river beads, and numerical

modeling of the effect of river beads on catchment-scale fluxes of water, nutrients, and organic carbon.

Uncertainties in the contribution of river beads to network-scale resilience to extreme climate events also involve issues of scale with respect to precipitation inputs or storm surges. Precipitation of sufficient intensity, duration, and spatial extent can overwhelm the retention of even a completely natural river network that still has numerous, fully functional river beads. Following the 1993 flood in the Upper Mississippi River basin, for example, questions arose as to whether the flooding would have been of such large magnitude and duration if the river network had not been extensively modified by land use and channel engineering (Hey and Philippi 1995). The consensus that emerged among hydrologists was that the sustained, widespread precipitation associated with that flood would have caused massive flooding even if the Mississippi River drainage had not been so extensively altered (e.g., Pitlick 1997). This consensus was largely based on expert judgment and inference, however, rather than network-scale hydrologic modeling. The characteristics of extreme events that can exceed the resilience and retention of river networks with diverse configurations of river beads remains largely unquantified. We also do not fully understand the nature (e.g., linear versus nonlinear) of the relationship between bead abundance and the network-scale function of beads. That is, is there a threshold bead abundance above which an increase in the number of beads has a diminished effect on the function they provide in the network, or does an increase in bead abundance or size linearly increase the magnitude of their function?

Gaps in understanding of river form and function related to river beads

Among the gaps in understanding that limit our ability to predict river resilience to extreme climate events and to restore resilience and retention to river networks are the following:

- The importance of the spatial distribution, size, and abundance of beads within a river network. Do beads in headwater streams create different levels of resilience or retention than beads in downstream portions of the river network? Do a few large beads create effects similar to many smaller beads?
- If bead size influences the level of resilience or retention associated with a river bead, is this effect linear or nonlinear? Comparing the changes in nitrogen export between a spatially extensive beaver meadow with multiple ponds in Table 1a versus a channel (Wegener et al. 2017) and a single beaver pond versus a riffle (Naiman and Melillo 1984) suggests that increasing the size and spatial heterogeneity of a river bead can result in a nonlinear increase in retention, but this question requires much more focused research.
- Quantitative studies that facilitate comparison of beads and strings within a single river are very limited in number and come from a small range of geographic areas (Table 1). How readily transferable or scalable are these results to other rivers?
- Within a river bead, what are the thresholds that maintain or restore river function? How much instream wood, for example, creates an anastomosing channel planform or significantly greater hyporheic exchange flow?
- What is the most effective way to restore physical or biotic drivers of bead function in diverse environments? Instream wood and beavers appear to underpin restoration strategies for forest streams in the North American Rocky Mountains, but a more natural sediment and flow regime may be critical to rivers of the U.S. Great Plains (e.g., Jacobson et al. 2009) and to rivers of the European Alps (Habersack and Piégay 2007; Surian et al. 2009).
- Is there some minimum size or abundance of river beads needed to ensure network-scale resilience to disturbances (Bernhardt and Palmer 2011), including potential increases in extreme climate events in future? That is, what is the nature of the relationship between bead size/abundance and the magnitude of their function in enhancing resilience at the scale of entire river networks?
- What is the threshold at which retention and resilience created by river beads no longer significantly influence flooding associated with extreme climate events? Is there such a threshold?
- What is the best strategy(ies) for restoring spatial heterogeneity in highly altered river networks where substantial reductions in the spatial and temporal variability of water and sediment fluxes, as well as the magnitude of sediment fluxes, have dampened river dynamics?

- How can we couple predictions of changes in extreme climate events with numerical models of river function such as nitrate dynamics or channel mobility?

In summary, greater quantitative understanding of the form and function of river beads holds substantial potential for improving river management and restoration in the face of continuing changes in land cover and climate, but significant knowledge gaps remain to be addressed.

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