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Leaky rivers: Implications of the loss of longitudinal fluvial disconnectivity in headwater streams

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ABSTRACT

Naturally induced longitudinal disconnectivity in the form of channel-spanning logjams creates backwaters along headwater streams that reduce velocity and transport capacity, create at least temporary storage sites for finer sediment and organic matter, and enhance biological processing and uptake of nutrients. Land uses that reduce wood recruitment and instream storage result in reduced stream complexity and increased longitudinal connectivity in headwater rivers. We examine three scales of naturally occurring longitudinal disconnectivity in headwater streams of the Colorado Front Range and the implications for channel process and form of historical alterations in disconnectivity. Basin-scale disconnectivity at channel lengths of 10^2–10^3 m results from downstream alternations between steep, narrowly confined valley segments with single-thread channels, and lower gradient, wider, valley segments with multi-thread channels. This variation in valley geometry likely reflects differences in average spacing between joints in bedrock outcrops, which influences bedrock weathering and erosion. Greater volumes of wood stored in the wide valley segments correlate with more closely spaced channel-spanning logjams and greater storage of fine sediments and organic matter. Reach-scale disconnectivity at channel lengths of 10^1–10^2 m results from the presence of numerous, closely spaced channel-spanning logjams, which cumulatively store substantial amounts of fine sediment and organic matter. The backwater effects associated with an individual jam can result in the accumulation of up to ~11 m^3 of fine sediment upstream from the jam, of which as much as 21% is organic matter. Unit-scale disconnectivity at channel lengths of 10^0–10^1 m results from the presence of an individual channel-spanning logjam, which locally alters bed gradient, substrate composition, bedform dimensions, and the transport of sediment and organic matter. The transport and storage of instream wood is a critical component of disconnectivity at all spatial scales examined. Land uses such as timber harvest, flow regulation, and placer mining that result in reduced wood recruitment or removal of instream wood appear to create an alternative stable state in which channels are unable to retain wood because of reduced debris roughness. The net effect of reduced longitudinal disconnectivity is increased transport of fine sediment and organic matter and reduced biological uptake of nutrients. The altered headwater streams become leaky with respect to fine sediments and nutrients.

1. Introduction

Ecologists, hydrologists, and geomorphologists emphasize the importance of connectivity in drainage basins. Drainage basins that have not been intensively altered by humans tend to have high-levels of connectivity. Connectivity can be conceptualized in terms of landscape connectivity (Brierley et al., 2006), in which individual landforms such as hillslopes and channels are closely coupled. Sediment connectivity (Fryirs et al., 2007) occurs where sediment can move rapidly from production sites on hillslopes through the drainage basin, as opposed to being retained in human-built dams or sediment detention basins. Hydrological connectivity (Kondolf et al., 2006; Bracken and Croke, 2007) is present where water and water-mediated fluxes of material, energy, and organisms move freely throughout the river network and between surface and subsurface components, again as opposed to being retained in human-built dams. Although connectivity is widely viewed as ecologically beneficial (Pringle, 2001, 2003; McGinness et al., 2002; Ward et al., 2002; Jenkins and Boulton, 2003; Tetzlaff et al., 2007), the temporal and spatial dimensions of connectivity are crucial. Artificially enhanced connectivity can create problems, for example, when water diversions facilitate migration of invasive species (Waters et al., 2002). Many river systems have naturally induced, longitudinal disconnectivity in the form of features such as logjams or beaver dams that produce temporary reductions in the downstream passage of water and sediment and facilitate storage of fine sediment and organic matter in valley bottoms (Burns and McDonnell, 1998). By creating backwaters that reduce velocity and transport capacity, jams and dams reduce longitudinal connectivity, but enhance lateral connectivity (Collins and Montgomery, 2001; Pollock et al., 2007; Burchsted

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et al., 2010). Aggradation in the backwater zone reduces channel cross-sectional area and promotes overbank flooding (John and Klein, 2004; Westbrook et al., 2010). A key distinction is that logjams and beaver dams do not form permanent, impassable barriers to downstream movement of materials, but rather punctuate this movement by forming temporary storage zones. Logjams and beaver dams can be readily overtopped and fail during high discharges, sending a pulse of water, sediment, and organic material downstream (Butler, 1995). While the dams and jams are intact, they increase habitat and biodiversity (Rolauffs et al., 2001), channel stability (Pollock et al., 2007), and the storage and biological processing of organic matter (Naiman and Melillo, 1984).

The most common human-induced alteration of river ecosystems is reduced connectivity associated with the construction of features such as dams and levees that are designed to completely restrict movement of water and sediment along a river at all discharges (Kondolf et al., 2006). Human activities can also increase connectivity via water diversions or, more commonly, removal of naturally occurring features including beaver dams, logjams, secondary channels and channel-margin irregularities, all of which reduce the rate and magnitude of downstream transport while they are present. Activities as diverse as beaver trapping, timber harvest, log floating, channelization, construction of transportation corridors, and urbanization result in reduced complexity and increased longitudinal connectivity in rivers (Wohl, 2001). In this paper we discuss altered connectivity in headwater mountain streams of the Colorado Front Range, where timber harvest and various forms of river management have resulted in reduced instream wood loads and consequent increases in longitudinal connectivity but reductions in lateral connectivity (i.e., floodplain-channel connectivity) within the river network. We also discuss the implications of these historical alterations in connectivity for channel process and form.

Numerous studies have investigated increased longitudinal connectivity in lowland, alluvial rivers along which levees and channelization have eliminated secondary channels and isolated floodplains (Schoof, 1980; Harvey et al., 1983; Shankman and Pugh, 1992). Mountain streams, such as those in the Front Range, tend to have greater longitudinal connectivity and high transport capacity for organic matter and gravel and finer sediment because steep, narrow valley geometry limits the extent of floodplains and secondary channels. Any localized form of disconnectivity that creates at least temporary storage of fine sediment and organics may, thus, be disproportionately important because it facilitates microbial uptake of nutrients (Battin et al., 2008) along river corridors that otherwise have limited opportunities for such uptake. If these forms of disconnectivity are reduced, a steep, headwater river can become leaky with respect to nutrients, transporting them rapidly downstream rather than allowing organisms to utilize the nutrients.

2. Study area

Our field data and conceptual model are based on the catchment of North St. Vrain Creek in Rocky Mountain National Park, Colorado (Fig. 1). The creek drains 250 km^2 of the Colorado Front Range, flowing east from its headwaters at 4046 m at the Continental Divide to 1945 m at the base of the range, where it enters the Great Plains and eventually joins the South Platte River. We focus on the headwater portion of the catchment, which drains approximately 80 km^2, and lies above the Pleistocene terminal moraine. This portion of the basin is underlain by Precambrian-age Silver Plume Granite (Braddock and Cole, 1990) and is covered by subalpine spruce-fir forest dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) (Veblen and Donnegan, 2005). Old-growth characteristics of this forest typically do not emerge for at least 200 years (Veblen and Donnegan, 2005). A mosaic of stand ages is present in the study area, including old-growth stands in which trees germinated prior to1654 A.D., and in 1654, 1676, and 1695, as well as younger forest in which trees germinated in 1880 and in 1978 (Sibold et al., 2006). Mean annual precipitation is 71 cm and stream flow is dominated by snowmelt, with an annual peak during May–June. A gaging station just downstream of the study area has been maintained since 1926; mean annual peak flow is 20 m^3/s, with a maximum peak discharge of 46 m^3/s in June 1941.

Bedrock (Precambrian biotite schist and granite; Braddock and Cole, 1990) is discontinuously exposed along the boundaries of North St. Vrain Creek and its principal tributaries, which are formed primarily in boulder- to cobble-sized sediment. Cascade, step-pool, plane-bed and pool-riffle morphologies (Montgomery and Buffington, 1997) are present along the river network. Downstream hydraulic geometry is poorly developed (Wohl et al., 2004) and instream wood is locally abundant (Wohl and Cadol, 2011).

Although North St. Vrain Creek is one of the least altered headwater tributaries of the South Platte River, beaver were trapped in the catchment during the first decades of the 19th century. Beaver trapping occurred throughout the upper South Platte River catchment, and when John Frémont passed through the region in 1842–43, he found many abandoned beaver lodges but few active colonies (Wohl, 2001). Although beaver populations have subsequently increased, they remain much lower than prior to the start of 19th century trapping. Other mountain tributaries of the South Platte experienced timber harvest, log floating, placer mining, flow regulation, and construction of transportation corridors adjacent to rivers during the latter half of the 19th century (Wohl, 2001). These activities altered the recruitment, transport, and storage of instream wood. The historical land uses and consequent changes in instream wood recruitment and retention, as well as other aspects of flow regime and channel morphology, are widespread throughout the U.S. Rocky Mountains, as well as other mountainous regions of the world (Wohl, 2006).

3. Naturally occurring longitudinal disconnectivity

We focus on naturally occurring disconnectivity in the channels of the North St. Vrain Creek network at three primary scales: the entire drainage basin (channel lengths of 10^2–10^3 m), channel reaches (lengths of 10^1–10^2 m), and channel units (10^0–10^1 m) (Table 1).

3.1. Basin-scale disconnectivity

Basin-scale disconnectivity results from downstream alternations between steep, narrowly confined valley segments with single-thread channels, and lower gradient, wider, valley segments with multi-thread channels (Fig. 2). Although there are transitional valley segments with intermediate gradient and width, the striking and abrupt downstream variations in valley geometry form an almost bimodal distribution of narrow and wide reaches. This variation in valley geometry likely reflects differences in the average spacing between joints in bedrock outcrops (Ehlen and Wohl, 2002; Wohl, 2008). Field measurements of joint spacing at bedrock outcrops along the valley bottom indicate that the steep, narrow valley segments have significantly more widely spaced joints than the other valley segments (Fig. 3). Differences in the average joint spacing between bedrock outcrops appear to correspond to differences in rock weathering and erodibility, which lead to differences in valley geometry.

Differences in valley geometry correspond to differences in main channel width, channel planform, bed gradient, volume of wood in the channel and on the floodplain, and the frequency of channel-spanning logjams (Table 1). The greater volumes of wood stored in the wide valley segments likely reflect greater recruitment opportunities from more extensive riparian forests (Wohl, 2011), as well as lower transport capacity. Wood recruited into the channel as a ramped piece (one end resting above the bankfull level) can initiate a channel-spanning logjam by trapping wood in transport. The logjam creates a backwater effect in a steep, narrowly confined channel segment that rapidly increases the hydrostatic force acting on the

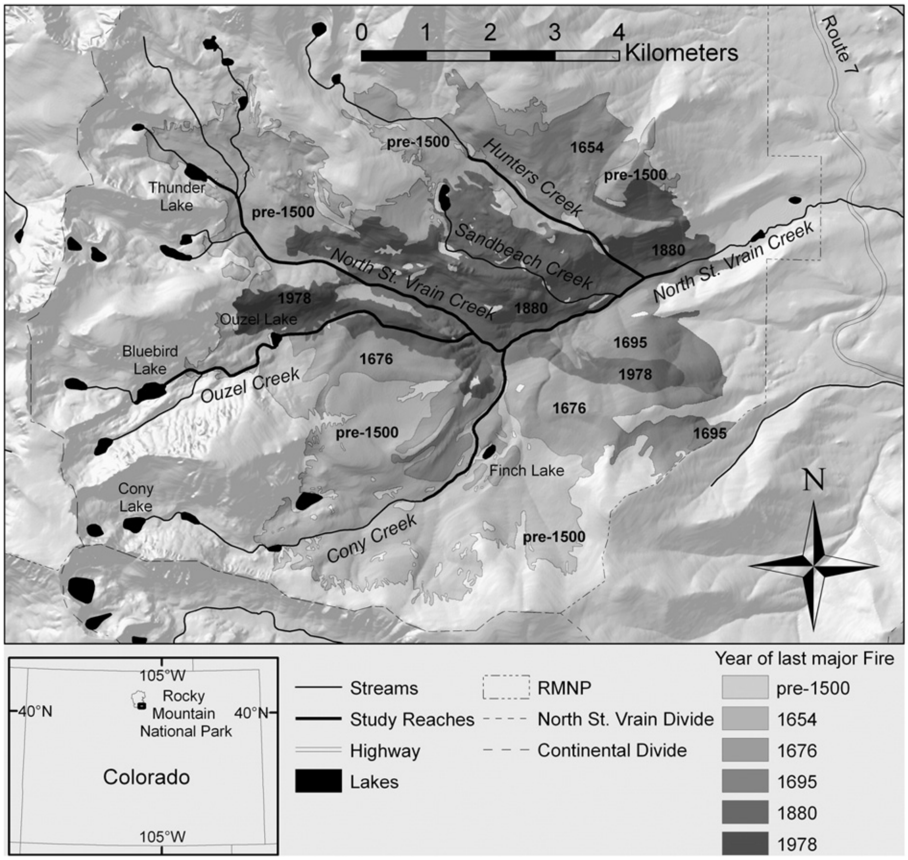

Fig. 1. Location map of the upper North St. Vrain Creek catchment within Rocky Mountain National Park, showing the stream network and forest stand ages. Map created by Daniel Cadol.

jam and enhances the likelihood of flow removing the jam (Wohl, 2011; Fig. 4). In contrast, the presence of a wide valley bottom and floodplain creates a safety valve. Backwater effects result in bed aggradation and greater depth of flow immediately above the jam. This causes overbank flow, which limits the increase in hydrostatic force on the jam by reducing further increases in the depth of flow and velocity in the vicinity of the jam. The jam is more likely to be persistent than a jam in a narrow, laterally confined valley segment. Overbank flow across an irregular floodplain surface can also concentrate in topographic depressions and initiate secondary channels, leading to a multi-thread channel planform. The much greater volume of wood stored at least temporarily in the wide, low gradient valley segments results in greater storage of fine sediments (<16 mm) and organic matter (Wohl, 2011), and the presence of hydraulically rough, shallow secondary channels across the floodplain further enhances opportunities for storage of wood, finer organic matter, and fine sediments. The downstream alternations in valley geometry, thus, correspond to downstream disconnectivity in transport of wood, finer organic matter, and fine sediment, which are preferentially stored in the wider valley segments. We designate steep, narrow valley segments as transfer reaches because they effectively transfer downstream most of the organic material and sediment of sand size or finer that enters them. Wide, low-gradient valley segments are storage reaches because organic material and fine sediment are at least temporarily stored here, facilitating microbial processing of the organic material (Battin et al., 2008).

3.2. Reach-scale disconnectivity

Reach-scale disconnectivity results from the presence of numerous, closely spaced channel-spanning logjams. Channel-spanning logjams

Table 1
Differing spatial scales of naturally occurring longitudinal disconnectivity in the North St. Vrain Creek catchment.

Scale	Length (m)	Time (y)	Description	
Basin	10^2–10^3	10^3–10^5	*Transfer reaches*[a]	*Storage reaches*
			single-thread channel	multi-thread channel (2–8 channels across valley, avg 3.6)
			8–10 m wide channel	14–18 m wide main channel
			15–25 m wide valley bottom	70–90 m wide valley bottom
			0.09 m/m avg gradient	0.03 m/m avg gradient
			avg. 3.8 m^3 wood/100 m channel	avg. > 17.4 m^3 wood/100 m channel
			avg. 0.5 m^3 wood/100 m floodplain	avg. 12.3 m^3 wood/100 m floodplain
			avg. 1 channel-spanning jam/100 m channel	avg. 2.6 channel-spanning jam/100 m channel
Reach	10^1–10^2	10^1–10^2	Channel-spanning logjams[b]: jam height 1–2 m, average peak flow depth across floodplain 0.4–0.7 m; cumulative instream sediment storage for multiple jams in a 100-m-long storage reach averages ~21 m^3, of which ~9% is organic matter	
Unit	10^0–10^1	10^0–10^1	0.8–10.8 m^3 of sediment stored in backwater created by each jam; the sediment stored upstream from a jam is 2–21% organic matter (mean 11%, standard deviation 14%)	

[a] Characterization of transfer and storage reaches based on a sample size of 10 transfer reaches and 6 storage reaches, each 100 m long.
[b] Characterization of logjams based on sample size of 9 jams.

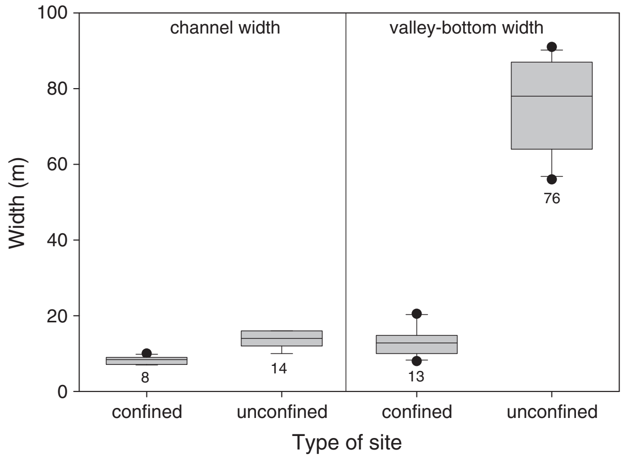

Fig. 2. Box plots illustrating channel width (left) and valley-bottom width (right) in laterally confined or narrow and laterally unconfined or wide valley segments in the North St. Vrain catchment. The top and bottom of each box represent the upper and lower quartile with the band between them representing the median. The ends of the whiskers are 1.5 times the interquartile range, a measure of statistical dispersion equal to the difference between the first and third quartiles. The dots located outside the whiskers are considered extreme values. Mean values for each population are listed below the box. Each population includes 11 data points taken at a similar drainage area of approximately 20 km^2. For both channel and valley-bottom width measurements, the two populations differ at a significance level of 0.05.

occur throughout the river network, but are most common and best-developed in the wider, lower gradient valley segments (Fig. 5). The average longitudinal spacing of jams throughout the network is difficult to predict because of the strong influence of local variations in wood recruitment and dimensions, which reflect spatial extent, age, and size of riparian trees, and in wood transport, which largely reflects valley and channel geometry. Stepwise linear regression analysis of jams along channels in old-growth forests indicates that drainage area and channel gradient correlate significantly with the downstream spacing of logjams (adjusted R^2 0.41, C_p 3.88), whereas drainage area and stand age correlate significantly with jam spacing when stream segments in younger forests are included (adjusted R^2 0.06, C_p 3.08) (Table 2). Each of these models, however, explains less than half of the variability in the downstream spacing of jams.

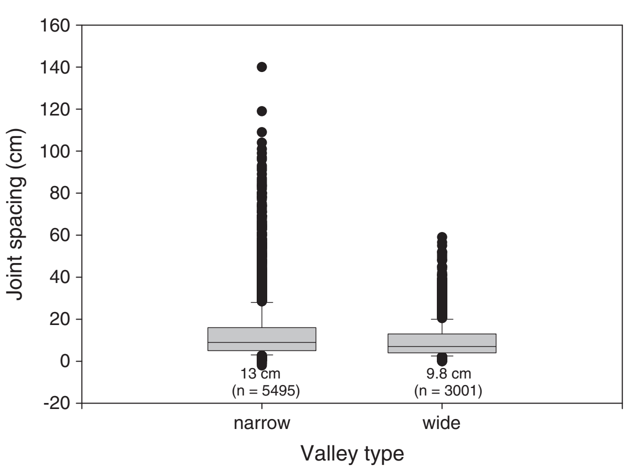

Fig. 3. Box plots illustrating average spacing between joints in bedrock outcrops along the walls of narrow and wide valley segments in the North St. Vrain catchment. The top and bottom of each box represent the upper and lower quartile with the band between them representing the median. The ends of the whiskers are 1.5 times the interquartile range, a measure of statistical dispersion equal to the difference between the first and third quartiles. The dots located outside the whiskers are considered extreme values. Mean values for each population are listed below the box, along with the number of joints measured (n). The two populations differ at a significance level of 0.05.

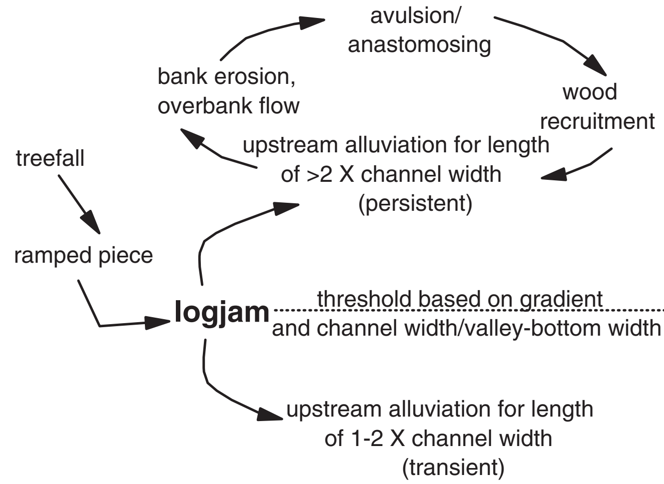

Fig. 4. Schematic illustration of conceptual model of characteristics of logjams in wide and narrow valley segments.

In the wide, low gradient valley segments, where jams are typically spaced 20 to 50 m apart, they cumulatively store substantial amounts of fine sediment and organic matter at channel lengths of tens to hundreds of meters. The backwater effects associated with a jam can result in the accumulation of up to ~11 m^3 of fine sediment upstream from the jam (average 8.2 m^3), of which as much as 21% is organic matter (Table 1). Samples of finer grained (pebble size and finer) bed sediment associated with jams contain substantially more organic matter than those from other zones of flow separation along the channel (Fig. 6). As a first-order approximation, we use the average value of ~2.6 jams/100 m to estimate ~385 m^3 of fine sediment and organic matter stored in association with jams along the ~1800 m of valley length occupied by the upstream-most population of multi-thread channels along North St. Vrain Creek. A substantial volume of sediment is also stored in logjams along secondary channels and across the floodplain, which consists of 0.5–1 m of sand and finer sediment and organic matter overlying a basal layer of cobbles and boulders. For storage reaches, we estimate a total volume of ~110,000 m^3 of fine sediment and organic matter stored

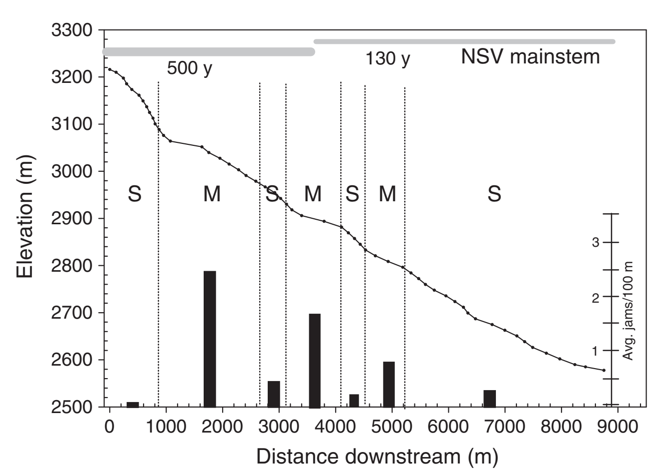

Fig. 5. Longitudinal profile of the mainstem North St. Vrain Creek, indicating alternating single-thread (S) and multi-thread (M) channel segments. Black bars at bottom of figure indicate number of channel-spanning logjams per 100 m of channel length (scale at right). Gray bars along top of figure show the average stand ages of the adjacent forest, in years. The most downstream multi-thread channel segment is partly relict and not as well-developed as the segments in the old-growth (500 y) portion of the catchment.

Table 2
Statistical models of downstream spacing of logjams.

Linear model for downstream spacing of logjams as dependent variable in streams draining old-growth forests		
Predictor variable	Coefficient	p-value
Drainage area	0.114	0.00447
Channel gradient	−5.15	0.01187
Linear model for downstream spacing of logjams as dependent variable in streams draining forests of diverse age		
Predictor variable	Coefficient	p-value
Drainage area	0.160	0.00102
Stand age	0.012	0.02324

upstream from channel-spanning jams and across the floodplain that these jams help to create. (Estimates of floodplain storage are based on valley-bottom width and average thickness of fine sediment present above the basal cobble-boulder layer in these valley segments.) In contrast, we use values of 1.4 m^3 of average sediment storage, 1 jam/100 m and narrower, thinner floodplain deposition to estimate a total volume of ~21,600 m^3 of fine sediment and organic matter stored in an 1800-m length of transfer stream reaches. These are relatively crude approximations, but they highlight the substantial differences between storage and transfer reaches of these headwater streams.

In addition to disrupting longitudinal connectivity, channel-spanning logjams facilitate lateral connectivity in the wider, lower gradient segments of valley by creating backwater effects that result in local sediment accumulation, loss of channel capacity, and enhanced overbank flow. Overbank flow helps to promote storage of fine sediment and organic matter through vertical accretion and through enhanced recruitment of riparian trees as bank erosion along secondary channels causes trees to fall into the channels. As noted in Table 1, the width of the valley bottom can reach nearly 100 m in portions of the upper catchment.

3.3. Unit-scale disconnectivity

Unit-scale disconnectivity results from the presence of an individual channel-spanning logjam, which locally alters bed gradient, substrate composition, bedform dimensions, and the transport of sediment and organic matter. Hyporheic exchange is likely much greater in these wedges of fine sediment than in the adjacent coarse-grained bed segments up- and downstream (Kasahara and Wondzell, 2003; Lautz et al., 2006; Wondzell, 2006; Hester and Doyle, 2008). Large pools also form in the backwater created by a jam, where additional wood is likely to be trapped and at least partially buried in the bed sediment. The presence of an individual jam creates pronounced local longitudinal disconnectivity in the transport of wood, finer organic matter, and fine sediment (Fig. 7). When a jam is partly or wholly breached, a headcut moves upstream through the wedge of sediment stored above the jam and the bed sediment in the thalweg changes from pebbles and sand to cobbles and boulders, although fine sediment may remain in storage along the channel margins. While intact, the jam can also facilitate localized overbank flooding in low-gradient valley segments and lead to locally split flow or multi-thread channels.

Summarizing the relations among the three scales of disconnectivity, we infer that longitudinal variation in the volume of instream wood reflects basin-scale controls on wood recruitment, transport, and storage. Instream wood then drives reach- and unit-scale disconnectivity by forming channel-spanning logjams that interrupt the downstream movement of wood, finer organic matter, and fine sediment (Fig. 8). Differences in joint geometry and rock erodibility control downstream alternations in valley geometry. Valley geometry, along with forest age, then strongly influences reach- and unit-scale disconnectivity, and precludes consistent downstream trends in channel geometry, bed grain size, or wood load (Wohl et al., 2004; Wohl and Cadol, 2011).

3.4. Persistence of longitudinal disconnectivity

The scales of longitudinal disconnectivity highlighted here differ in duration. Patterns of basin-scale longitudinal disconnectivity, because they are forced by bedrock weathering and erodibility, likely persist for millions of years (Table 1). The upper portions of North St. Vrain Creek are deeply entrenched; where steep, narrow, single-thread channels are present, the channel typically lies 60–80 m below the top of the adjacent valley wall.

Patterns of channel-spanning logjams are likely to be more transient in response to changes in the recruitment of wood associated with wildfires, blowdown, or insect infestations, and changes in transport associated with above-normal snowmelt floods (Wohl and Goode, 2008; Marcus et al., 2011). A decade-long study of interannual movement of wood in channel segments flowing through younger forests in this catchment indicated an average residence time of only 3.4 years per piece, although this number was slightly longer for pieces incorporated in jams (Wohl and Goode, 2008). As might be expected, greater wood movement occurred during years with higher peak flows. We began annual resurveys of five large logjams

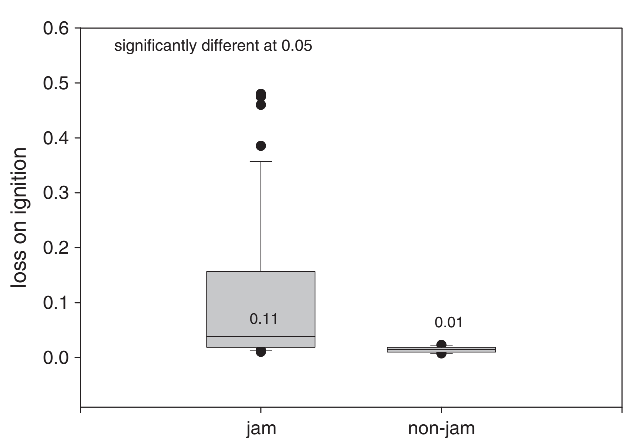

Fig. 6. Box plots of percent organic matter, as measured by loss on ignition of sediment sample, for fine sediment associated with channel-spanning logjams and those not associated with jams. The horizontal line within each box indicates the median value, which is also listed above the line. Box ends are the 25th and 75th percentiles.

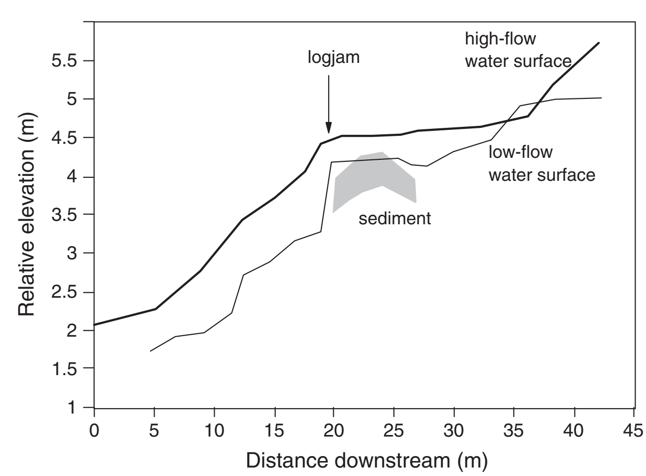

Fig. 7. Illustration of downstream discontinuity in water surface and bed surface associated with sediment wedge upstream from logjam (gray shading), as surveyed at a channel-spanning logjam along Cony Creek, a tributary of North St. Vrain Creek.

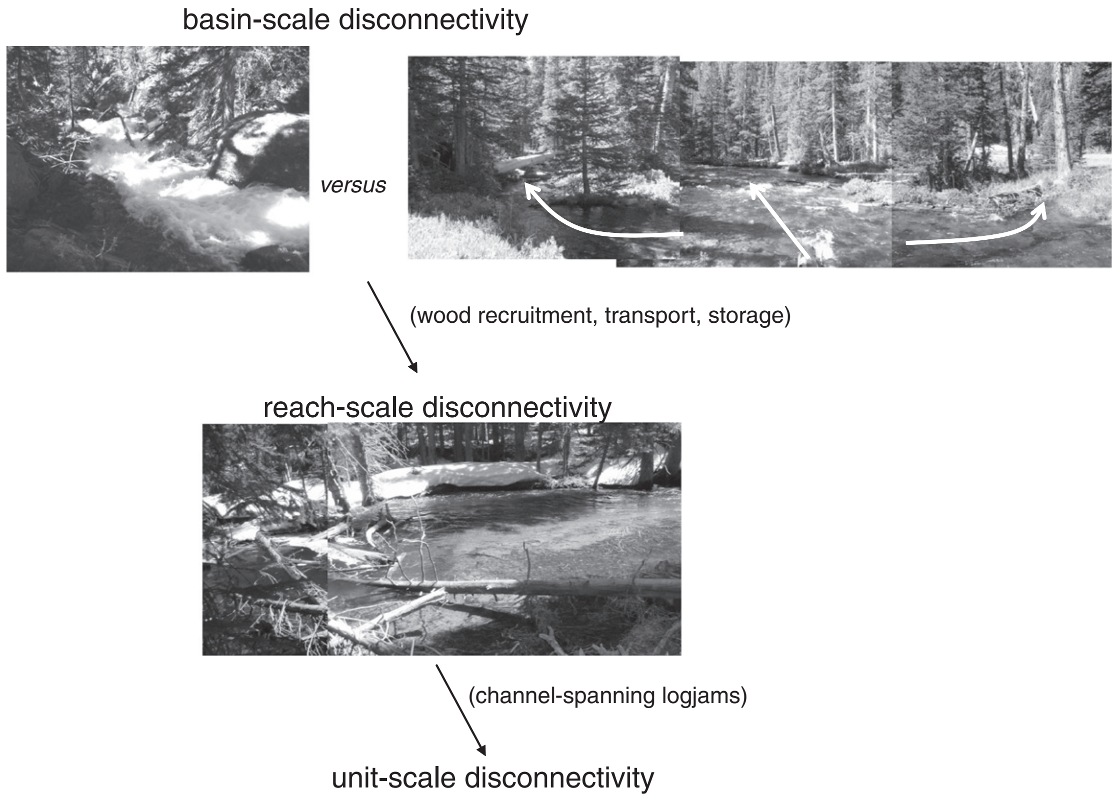

Fig. 8. Schematic illustration of the different scales of naturally occurring longitudinal disconnectivity in the upper North St. Vrain Creek catchment, Colorado. In the photographs illustrating basin-scale disconnectivity, the channel at left is ~10 m wide. Multi-thread channels in the view at the right are highlighted with white arrows and the main channel is ~15 m wide. The photograph illustrating reach-scale disconnectivity is a view across the backwater created by a channel-spanning logjam along North St. Vrain Creek just prior to annual peak flow. Flow is from right to left, and the wood at left is part of the logjam. The channel is ~12 m wide here. Note the accumulation of fine organic matter (conifer needles and cones) at lower right. The water surface at the far edge of the channel is just beneath a snowbank.

three years ago (Wohl, unpub. data). Only two of those jams now remain, partly because of very large snowmelt peak flows during the past two summers. Individual jams, thus, are relatively transient. Individually tagged logs indicate that, in a reach with multiple, closely spaced jams, much of the material released downstream when a jam is breached or removed is trapped in downstream jams. We estimate that, on average, a jam persists only a few years in a steep, narrow channel segment and perhaps one to two decades in a wide, low gradient segment. The average number of jams per length of channel is likely to be more consistent at timespans of a few years to several decades; although individual jams in the study reaches have broken up during the past three years, new jams have formed. At longer timescales of several decades, the average number of jams is likely to change significantly in response to substantial changes in recruitment. Considering only stand age, for example, and not valley geometry, the greatest frequency of jams occurs in a portion of the North St. Vrain tributary Ouzel Creek, which was burned in 1978 (Fig. 9). The 1978 fire was sufficiently intense to completely kill the trees adjacent to portions of the creek. Many of these trees remained standing and have been gradually falling; 33 years later, standing dead trees remain adjacent to the stream. The increase in wood recruitment over this 33-year period results in very high volumes of wood along and immediately downstream of portions of Ouzel Creek burned in 1978. At least a slight decrease in logjam frequency will likely occur during the next few decades because of dramatically reduced recruitment. Trees that have germinated since the fire are ≤2 m in height because of slow rates of growth at this high elevation site (3040–2920 m). Unburned stands of old-growth forest upstream from the fire zone will continue to supply wood via downstream transport. Because wood decays very slowly in this cold, dry climate, we do not expect instream wood loads to decline to nothing. Instead, it seems reasonable to assume that the frequency of channel-spanning jams will eventually decrease to values seen in older forest stands (Fig. 10), each of which experienced wildfires in the past. In this respect, the unmanaged stream segments along burned portions of Ouzel Creek differ significantly from headwater streams elsewhere in the region from which instream wood has been directly removed in association with timber harvest, placer mining, flow regulation, log floating, and other human activities. Instream

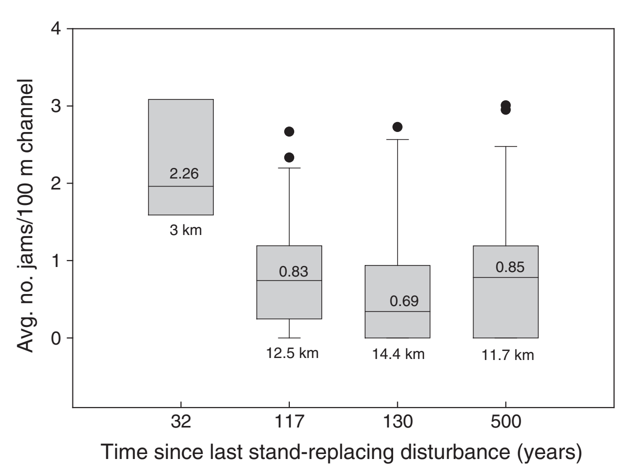

Fig. 9. Box plots illustrating number of jams per 100 m of channel in streams flowing through forests of different stand ages. The top and bottom of each box represent the upper and lower quartile with the band between them representing the median. The ends of the whiskers are 1.5 times the interquartile range, a measure of statistical dispersion equal to the difference between the first and third quartiles. The dots located outside the whiskers are considered extreme values. Mean values for each population are inside the box. Total stream length sampled is listed below each box in kilometers.

wood in these managed streams may go to very low or essentially zero values because active removal of wood decreases the debris roughness (Braudrick and Grant, 2001) or trapping efficiency of the stream for naturally recruited wood entering the stream after the management activities or from upstream, unmanaged stream segments.

4. Historical loss of longitudinal disconnectivity

As noted previously, many of the adjacent headwater catchments in the Colorado Front Range have experienced historical resource use that effectively altered the dynamics of instream wood. All of the headwater tributaries of North St. Vrain Creek flow primarily through old-growth forest, except for the portion of Ouzel Creek burned in 1978. Nearby channels with similarly wide, low-gradient valley geometry that flow through younger forest do not have a multi-thread planform. Younger forests have significantly lower values of riparian basal area (a measure of the volume of standing wood available to be recruited into the channel) and smaller intermediate and maximum piece diameters for populations of instream wood (Wohl, 2011). Old-growth forest that produces large diameter pieces of instream wood that are relatively immobile and facilitate the formation of persistent jams appears to be necessary to create a multi-thread channel planform even in wide, low gradient valley segments. In the absence of old-growth forest and sufficient instream wood, reach- and unit-scale disconnectivity decrease as channel-spanning logjams become smaller and/or more widely spaced downstream.

During a 2010 summer survey of 393 channel-spanning logjams in the upper North St. Vrain catchment, we found that >80% were 'keyed', or formed around, ramps or bridges (pieces of instream wood with both ends resting above the bankfull level) where the channel flowed through old-growth forest. Ramps and bridges, because they have at least a portion of the length resting above the average annual high flow, tend to be less mobile than pieces completely contained within the active channel. The average downstream spacing of ramps and bridges varies substantially among the three channel populations (Table 3). Not every ramp or bridge creates a channel-spanning jam, but the average downstream spacing of such jams also varies among the three channel populations. These results suggest that ramps and bridges are particularly important in creating and maintaining reach- and unit-scale disconnectivity in channels flowing through old-growth forest.

We view ramps and bridges as creating a form of debris roughness. Braudrick and Grant (2001) used debris roughness to characterize trap efficiency during flume experiments on wood transport. They

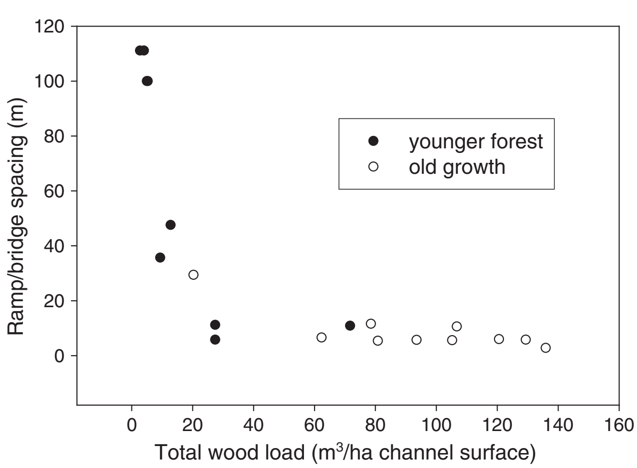

Fig. 10. Downstream spacing of ramps and bridges versus instream wood load for 17 1-km-long stream segments flowing through forests of different age in the Colorado Front Range. Data include sites from outside of the North St. Vrain Creek catchment.

Table 3
Average characteristics of ramps and channel-spanning logjams.

Forest age and channel planform type	Avg downstream spacing of ramps and bridges (m)	Avg no. channel-spanning logjams/100 m channel
Old-growth, multi-thread	6.2	2.6
Old-growth, single-thread	3.3	0.9
Younger, single-thread	6.4	1.0

attributed debris roughness in their experimental channels to values of such ratios as log length to channel width, log length to radius of channel curvature, and log buoyant depth to average flow depth. They also noted that variables such as relative grain submergence and standard deviation of channel width likely influence the ability of a channel to trap wood in transport. Variation in channel width clearly influences basin-scale disconnectivity, as discussed above. Based on the high percentage of jams keyed by ramps and bridges, we infer that ramps and bridges effectively increase debris roughness and trap efficiency at reach- and unit-scales. If other factors are equal, a channel with closely spaced ramps and bridges is like a highway with heavy traffic flow on which an accident occurs. The accident disrupts the movement of other vehicles, sometimes for long periods of time. Similarly, wood in transport downstream is more likely to keep moving along a relatively unobstructed channel. More closely spaced obstacles formed by ramps and bridges increase the likelihood that wood in transport will be at least temporarily lodged against the obstacles and, thus, help to further disrupt transport of other pieces of wood.

The inferred importance of debris roughness in forming channel-spanning logjams leads to the possibility that streams in the study area have alternative stable states with respect to wood. Although wood load varies through time in unmanaged channels, it probably does not decline below some minimum because of slow rates of decay; even a debris flow along the channel would be unlikely to completely remove all wood along extensive lengths of channel. Wood in managed channels, in contrast, was in many cases completely removed during 19th-century timber harvest, placer mining, and log floating. In some managed channels, wood is still removed to prevent damage to infrastructure such as bridges and water intakes or to facilitate recreational boating. Recruitment of new wood can be curtailed by timber harvest or construction of transportation corridors near rivers. In each scenario, the debris roughness and trap efficiency of the channel is substantially reduced. We hypothesize that, following extensive or complete removal of instream wood, transport capacity in all but the smallest headwater channels is so high that any newly recruited wood is less likely to be retained in the channel than it would be in an unmanaged channel with abundant instream wood. This suggests that channels could remain wood-poor for many decades following artificial removal of instream wood, an inference that is supported by the longer spacing of ramps and bridges and lower frequency of channel-spanning jams in channels flowing through wide, low gradient valley segments with younger forest when compared to channels with analogous valley geometry in old-growth forest (Table 2). A wood-poor channel is effectively stable or self-perpetuating because of the reduced ability to trap newly recruited wood, and a wood-rich channel is equally stable because of its ability to trap newly recruited wood even as some trapped wood is remobilized and continues downstream. The hypothesis of alternative stable states is supported by the apparent threshold in a plot of ramp and bridge spacing versus instream wood load (Fig. 10). A dataset based on wood surveys of 1-km stream reaches in forests of differing ages indicates that ramps and bridges spaced more widely than ~20 m along the stream correspond to low instream wood loads.

In the absence of abundant instream wood and channel-spanning logjams, reach- and unit-scale disconnectivity decrease, and lateral disconnectivity increases. Channel planform diversity declines as multi-thread channels no longer form in connection with flow forced overbank at logjams. Pool volume declines and channels are more likely to have relatively consistent cobble to boulder size substrate with plane-bed or step-pool morphology. Diversity, abundance, and stability of instream and riparian habitat decrease. Storage of fine sediment and organic matter decline substantially, along with the ability of instream microbes and invertebrates to biologically process carbon (Battin et al., 2008). Headwater channels, once characterized by hydraulic complexity and numerous storage reaches, become leaky with respect to organic matter, carbon, and other nutrients.

The scenarios described for North St. Vrain Creek are not unique to the Rocky Mountains in Colorado. River networks in forested mountainous regions around the world have undergone analogous changes in forest cover and resource use, and have likely experienced substantial declines in wood load and the frequency of channel-spanning logjams. River networks play an important role in the global carbon cycle (Stallard, 1998; Battin et al., 2008, 2009; Hilton et al., 2008a, 2008b) because storage in rivers can increase the residence time of organic carbon during downstream transport. The amount of carbon that rivers deliver to the oceans is only a fraction of the carbon entering rivers from terrestrial ecosystems; recent global compilations suggest an average flux of 2.7 Pg C/year from land into rivers, lakes, and wetlands, with 1.2 Pg C returned to the atmosphere, 0.6 to the geosphere, and 0.9 to the oceans (Aufdenkampe et al., 2011). Headwater streams are particularly influential because they receive most of the terrestrial carbon inputs from upland vegetation, regolith, and bedrock (Battin et al., 2008; Hilton et al., 2008a). Widespread decreases in the complexity of headwater channel boundaries and hydraulics that result in decreased storage and biological processing of organic matter can, thus, have important global consequences for the carbon cycle by increasing the transport of terrestrial and fossil carbon to oceans. Stream restoration that increases instream wood loads and the occurrence of channel-spanning logjams through passive measures of enhanced recruitment of wood to streams or active measures such as engineered logjams, can enhance aquatic and riparian habitat and productivity, as well as increasing the retention and biological uptake of carbon, nitrogen and other nutrients.

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