Biotic Drivers of Stream Planform: Implications for Understanding the Past and Restoring the Future

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Traditionally, stream channel planform has been viewed as a function of larger watershed and valley-scale physical variables, including valley slope, the amount of discharge, and sediment size and load. Biotic processes serve a crucial role in transforming channel planform among straight, braided, meandering, and anabranching styles by increasing stream-bank stability and the probability of avulsions, creating stable multithread (anabranching) channels, and affecting sedimentation dynamics. We review the role of riparian vegetation and channel-spanning obstructions—beaver dams and logjams—in altering channel–floodplain dynamics in the southern Rocky Mountains, and we present channel planform scenarios for combinations of vegetation and beaver populations or old-growth forest that control logjam formation. These conceptual models provide understanding of historical planform variability throughout the Holocene and outline the implications for stream restoration or management in broad, low-gradient headwater valleys, which are important for storing sediment, carbon, and nutrients and for supporting a diverse riparian community.

Keywords: stream planform, riparian vegetation, beaver, old-growth forest, restoration

Process-based restoration of fluvial systems is intended to create a dynamic, self-sustaining environment in which the root causes of ecosystem change are targeted and in which restoration actions are matched to local potential (Palmer et al. 2005, Beechie et al. 2010). Geomorphologists and ecologists acknowledge that restoring physical–biotic interactions is fundamental to process-based restoration, but a full understanding of these interactions is commonly lacking. From a geomorphic perspective, a full understanding must include changes in physical–biotic interactions over hundreds to thousands of years, because these long-term interactions can continue to influence contemporary process and form. Here, we explore physical–biotic interactions that influence channel planform within the context of the historical range of variability. *Channel planform* refers to two-dimensional stream geometry as seen from above. Planform both influences and responds to physical and biotic processes in riverine systems and also provides a master variable on which to focus self-sustaining, process-based stream restoration. The historical range of variability includes time periods prior to intensive human resource use—in the examples explored in this article, the Late Holocene to approximately 1800 CE. Conceptualizing the historical range of variability of physical–biotic interactions provides insight into both the longer-term range of riverine forms and processes under a similar hydroclimatic regime and the underlying landscape template for restoration. Along the continuum of restoration from purely process-based modeling to restoring to a reference condition, analysis of the historical range of variability of channel planform bridges these extremes by to reconstruct the past without requiring all biotic and physical processes and their interactions to be fully understood, a requirement that can be very difficult to meet in many systems.

Biotic influences on stream planform

Stream planform is typically characterized as a *single-thread channel* or as a *multithread channel*, with secondary channels that branch and rejoin downstream. Single-thread channels are further distinguished as *straight* or *meandering* on the basis of sinuosity, which is the ratio of a channel's length to its straight-line distance; a meandering channel has a sinuosity greater than 1.5. Multithread channels can be differentiated as *braided channels*, in which flow is separated by bars within a defined channel, or as *anabranching channels*, in which individual channels are separated by vegetated or otherwise stable bars and islands that are broad and long relative to the width of the channels and that divide flows at

BioScience 63: 439–452. ISSN 0006-3568, electronic ISSN 1525-3244. doi:10.1525/bio.2013.63.6.6

discharges up to bank-full levels. Interpretation of the factors governing stream planform has evolved from an emphasis on valley slope, discharge, and sediment load (Leopold and Wolman 1957) to incorporation of the effects of biotic influences, such as stream-bank vegetation (Tal and Paola 2007, Braudrick et al. 2009, Gurnell et al. 2009). Although there are no fluvial forms that exist only in the presence of biotic influences and thus indicate a "signature of life" (Dietrich and Perron 2006), certain channel types have a higher probability of forming with the presence of biota, as is illustrated by the emergence of narrow, less mobile channels with the evolution of terrestrial plants during the Paleozoic (Gibling and Davies 2012).

Several types of biota profoundly affect channel planform, including live and dead vegetation and ecosystem engineers, such as beavers. Flume and field evidence show that riparian vegetation sufficiently increases stream-bank cohesion and overbank roughness and the associated sediment deposition to cause braided channels to transition to a meandering or anabranching planform (Nadler and Schumm 1981, Tal and Paola 2007, Braudrick et al. 2009). Persistent logjams not only cause local in-channel changes in hydraulics and sediment deposition beneficial for fish habitat but also promote avulsions and anabranching (Abbe and Montgomery 2003, Wohl 2011a, Collins et al. 2012). Formation of anabranching can promote positive feedbacks through additional sources of wood input and additional channel length for avulsions and has implications for the storage of sediment and organic material, including carbon and coarse particulate organic material (Wohl et al. 2012). Similar to logjams, beaver dams facilitate avulsions and anabranching (Woo and Waddington 1990, John and Klein 2004, Burchsted et al. 2010, Polvi and Wohl 2012).

Stream planform reflects interactions between the timescales of biotic processes—for example, the growth rate of an individual or the evolution of groups of species—and geomorphic processes of disturbance frequencies and relaxation rates. Planform can adjust over time spans ranging from less than a few decades to millennia. The sedimentary record shows a surge in the occurrence of meandering channels in the middle Paleozoic (approximately 400 million years ago), coincident with the emergence of terrestrial plants with definitive roots (Gibling and Davies 2012). This shift in channel planform highlights a major turning point in landscape and biotic evolution. Other channel planform changes may happen over shorter timescales but are nonetheless important for landscape evolution, sediment dynamics, hydrologic connectivity, and ecological function and form. Invasive plant species can affect channel planform within decades, especially if the hydrologic regime is also altered, usually by hydropower installations. The combination of declines in peak and mean flows and the invasion of nonnative riparian *Tamarix* species has caused channel narrowing of more than 50% in 60 years along the Rio Grande in the Big Bend region in Texas (Dean and Schmidt 2011). Crack willow and tree lupin have changed braided rivers to a meandering planform downstream of hydroelectric dams in New Zealand by increasing stream-bank cohesion and reducing overbank velocities (Caruso 2006). These examples illustrate anthropogenically induced channel changes occurring in less than a century. Naturally occurring planform evolution can also occur on scales relevant to people and society, within years to decades, which can have lasting effects on ecological communities and on hydrologic and geomorphic processes.

Understanding current and past biotic–geomorphic interactions provides guidelines for ecological and stream restoration, because (a) current stream planform reflects not only current biotic–physical conditions and interactions but also the legacy effects of past conditions and (b) stream planform not only provides the physical template for ecological processes but also drives disturbance regimes and local hydrologic conditions on shorter temporal scales. We illustrate these points using a case study of biotic influences on multithread streams.

Objectives

In this article, we review the role of riparian vegetation and channel-spanning obstructions—beaver dams and logjams—in altering channel–floodplain dynamics. We develop conceptual models of channel planform response to diverse combinations of vegetation and beaver populations and to old-growth forest that controls logjam formation. These conceptual models allow us to infer historical conditions of channel planform during the Holocene along the Colorado Front Range (CFR) in the southern Rocky Mountains, using known reconstructions of climate, disturbances, and the presence or absence of beavers from the sedimentary record. In other words, we develop conceptual models of stream planform in relation to variation in climate and in valley geometry and biotic drivers. The conceptual models enhance our understanding of the historical range of variability of channel planform within current hydroclimatic conditions. In this context, the time period for the historical range of variability is the Late Holocene prior to resource use by people of European descent, which began circa 1800 CE. We use this historical analysis to determine potential reference conditions and possible future trajectories for channel planform and ecological condition, in addition to the implications for stream and riparian restoration.

The CFR provides an ideal case study in which abundant geomorphic, climatic, and ecological data are available without the area's being unique in terms of sediment dynamics, flows, and biotic interactions. Therefore, the analyses summarized in this article can be applied to systems with a mix of cohesive (silt and clay) and noncohesive (sand, gravel, cobble) sediment and interacting biotic factors that create channel-spanning obstructions.

Headwater streams in the Colorado Front Range

The CFR extends north from central Colorado to the border with Wyoming and east from the Continental Divide to the margin of the Great Plains. The region is underlain by Precambrian crystalline rocks (Braddock and Cole 1990), which have relatively slow rates of weathering, erosion, and sediment supply to the valleys. Above 2300 meters (m) in elevation, the flow regime is dominated by snowmelt, whereas lower elevations have snowmelt and flash floods caused by summer convective storms (Jarrett 1990).

Pinedale glaciation in the CFR extended down to 2300–2400 m in elevation and ended circa 10,000–15,000 years ago, depending on the elevation (Madole 1980, Madole et al. 1998). Postglacial warming lasted approximately 1000 years, with warmer-than-contemporary summer and winter temperatures (Elias 1996). The Altithermal period (6500–3500 years ago) had warmer summers, colder winters, and less precipitation than the present has (Benedict 1979, Short 1985, Elias et al. 1986, Elias 1996, Benedict et al. 2008). The tree line stood approximately 150 m higher than it does today. Snowmelt-driven spring floods were higher than at any other time in the Holocene for approximately 1000 years directly following the Altithermal period (Madole 2012). Finer-scale patterns revealed in dendrochronological records indicate periods of drought in the early 1700s, mid-1800s, and late 1800s, with smaller-magnitude droughts in the mid-1900s (Woodhouse 2001).

The contemporary elevational ecozones in the CFR include lower and upper montane zones (1830–2350 m and 2440–2740 m, respectively), a subalpine zone (2740–3450 m), and tundra above 3450 m (Marr 1964, Veblen and Lorenz 1991). Major shifts in climate cause the transitions between ecozones to shift in elevation. The headwater valleys on which we focus here have probably oscillated between the montane and subalpine zones as regional climate has fluctuated. The specific riparian vegetation species of *Alnus incana* (gray alder), *Betula occidentalis* (water birch), *Populus tremuloides* (quaking aspen), *Populus angustifolia* (narrowleaf cottonwood), and *Salix* spp. (willow) are common in both of these zones (Veblen and Lorenz 1991, Polvi et al. 2011).

We focus on the headwater region (approximately first- to fourth-order streams) of a mountainous basin where the valley geometry exhibits substantial longitudinal variability (Wohl 2001). We designate steep, narrow bedrock gorges in which channel width equals valley-bottom width as *confined valley segments.* Low-gradient valleys in which the active channel occupies only a small portion of the total valley-bottom width are *unconfined valley segments. Partly confined valley segments* are intermediate in width and gradient. Unconfined valleys occupy 25% of the total channel length but store 90% of the alluvial sediment and 75% of the floodplain carbon (Wohl et al. 2012). Our analyses are focused on unconfined valleys in which interactions between physical processes and biota can create unique, persistent, anabranching channels. Although not all unconfined valleys have anabranching channels, this channel planform occurs only in these valley segments. All other valley segments have a single-thread stream planform. Our observations indicate that anabranching streams in the CFR occur only in the presence of one of two biotic drivers: active beaver colonies or old-growth forest. Which biotic factor drives anabranching within an unconfined valley is hypothesized to be a function of the dominant vegetation type (conifers or deciduous riparian shrubs and trees) and whether beavers are or old growth is able to establish on a site first on the basis of primary plant succession processes. Once either beavers or old-growth conifer forests establish, they create a self-enhancing feedback by altering hydrologic and geomorphic processes, promoting growth of the dominant vegetation type. The original vegetation type is likely to be a function of several influences, including riparian water tables, disturbance history, primary succession, and the degree to which valleys are laterally unconfined. Very broad valleys (500–1500 m in width) that can support large populations of beavers are commonly found just upstream of terminal moraines, where riparian shrubs and trees are likely to dominate because of a higher water table and less shading. Locally high and longitudinally discontinuous water tables occur along these mountain streams even in the absence of channel-spanning obstructions, and the presence of high water tables facilitates the growth of the vegetation that beavers eat. Disturbances such as wildfires, avalanches, blowdowns, and insect infestations can create openings in the forest that favor pioneer species such as aspen, which is a preferred food for beavers.

Stream planform and beavers

The only animal documented to significantly influence channel planform is the beaver (*Castor canadensis* in North America; *Castor fiber* in Europe). The beaver is a large rodent that builds dams from wood and sediment; these dams reduce stream velocity and trap sediment upstream (Gurnell 1998). Although beavers are not responsible for a persistent, global shift in fluvial landforms, such as that by vegetation during the Paleozoic Era, they alter stream environments by damming channels and creating backwaters. These ecosystem engineers also alter riparian environments in low-gradient valleys where extensive backwater and overbank flooding associated with beaver dams can maintain high riparian water tables and limit the encroachment of upland plants (Westbrook et al. 2006). Habitat alteration by beavers increases the abundance and biodiversity of, for example, riparian species, aquatic macroinvertebrates, and bird species. Beaver-like species with the capacity to cut trees have been present for at least 25 million years (Rybczynski 2007). Estimates of populations for pre-European settlement North America range from 60 million to 400 million beavers (Naiman et al. 1988), and beavers were once abundant in the forested portions of Europe. Consequently, the cumulative effect of beaver activities on floodplain processes and channel planform is substantial.

Most studies on beaver effects, although they span only a few seasons, show a clear effect on channel gradient, velocity, sedimentation, and riparian vegetation (e.g., Butler and Malanson 1995, Gurnell 1998, Westbrook et al. 2006).

Seasonal sedimentation rates can exceed 0.2 m per year, as is evidenced in studies in various locations across North America (Butler and Malanson 1995, Pollock et al. 2007). Holocene sedimentation caused by beavers within low-gradient segments of mountain valleys in the CFR, although not impressively large in magnitude (with a mean thickness of 0.25 m, ranging from 0.05 to 1.2 m), constitutes a significant portion of the total postglacial sediments (30%–50% of the 2-m-thick alluvium; Kramer et al. 2012, Polvi and Wohl 2012). Anabranching channels with multiple dammed ponds, which trap a significant amount of fine sediment in unconfined valleys, were described as a *beaver-meadow complex* as early as the mid-1900s (Reudemann and Schoonmaker 1938, Ives 1942).

Overbank flooding and the subsequent avulsions around beaver dams contribute to the formation of a more complex anabranching channel network than would develop without beavers, as has been observed in diverse fluvial environments throughout North America and Europe (Woo and Waddington 1990, John and Klein 2004, Green and Westbrook 2009, Polvi and Wohl 2012). Beaver dams create backwater effects that enhance sediment deposition, lowering water storage capacity upstream of dams, and promote overbank flows, especially during early summer snowmelt floods. Beaver-affected areas are particularly prone to new channels being formed during overbank flows, because low-lying canals dug by beavers are present within the floodplain, which is connected to the ponds and nearby side channels. Because beaver dams allow some flow and are not completely sealed—as most anthropogenic dams are (Burchsted et al. 2010)—streamflow bifurcates and does not completely change course or abandon the original channel. A positive feedback develops in broad valleys with anabranching channels formed by beaver dams: Beavers create additional habitat for themselves from the ponded areas and by providing additional channel length that can be dammed, thus trapping more fine sediment (Polvi and Wohl 2012) and maintaining high riparian water tables that favor willow (*Salix* spp.) and other woody riparian species (e.g., *Populus* spp.) that provide a primary food source for the beavers (Westbrook et al. 2006).

Fine sediment ponded in the channel and deposited overbank is incorporated into stream banks as migrating and avulsing channels constantly rework stored sediments (figure 1). Storage and incorporation into stream banks of fine, cohesive sediment (clay and silt) influence channel dynamics, because stream banks composed of cohesive sediment are less likely to fail (Thorne 1982). When failure does occur, the reduced stream power associated with secondary channels and localized ponding is less likely to remove material at the toe of the bank, which reinforces the stream bank against further failure. Beaver dams not only promote the formation of anabranching while the area is maintained by the beavers but also create long-term, persistent effects after the beavers leave the area. Although vegetation can trap fine sediment on floodplains, which affects channel migration (Parker et al. 2011), the volume of cohesive sediment trapped in beaver ponds can be much greater. Furthermore, abandoned dams that are incorporated into the stream bank create a highly reinforced bank that severely limits channel migration and causes a combination of bed incision and a very high-angle bend in the channel.

Stream planform and old-growth forest

Old-growth subalpine forest requires at least 200 years to develop (Veblen 1986). Large-diameter logs recruited from old-growth forest into low-gradient channel segments can create closely spaced, persistent channel-spanning jams that effectively trap other wood in transport (Wohl 2011b, Wohl and Cadol 2011). The majority of these jams form around a relatively immobile ramp (one end resting above the active channel and commonly anchored to the bank by a partially buried root wad) or bridge (both ends resting above the active channel) piece. Backwater zones upstream from logjams accumulate sediment, and snowmelt floods are more likely to flow overbank near jams, creating secondary channels along which bank erosion and relatively shallow flow recruit and trap additional wood. Fine sediment and organic matter are deposited behind jams and across the floodplain in thicker sequences than in adjacent single-thread valley segments (Wohl et al. 2012). Streams flowing through younger forests do not have enough in-stream wood or closely spaced, persistent logjams to create the extent and duration of overbank flows necessary to maintain secondary channels.

If old-growth forest is removed through natural processes, such as wildfire, blowdown, or insect infestation, in-stream wood loads remain high, and anabranching channels are more likely to persist until the forest regrows, particularly if some standing dead trees remain for decades following the stand-killing event. The removal of old-growth forest through timber harvest, which is likely to occur in conjunction with the removal of in-stream wood, reduces the ability of the channel to trap and retain wood in transport (Wohl and Beckman 2011). The lack of channel-spanning logjams and their associated overbank flows causes the anabranching channel to assume a single-thread planform until sufficiently closely spaced, less mobile in-stream wood pieces such as ramps and bridges can begin once again to trap wood and create persistent jams.

Stream planform and stream-bank vegetation type

The type of stream-bank vegetation plays a large role not only in directly controlling the beavers or old-growth conifer population but also in determining the channel processes and thus planform, both before one of the main biotic drivers of anabranching can establish and while a dynamic anabranching system is active. Vegetation that has roots with higher tensile strengths and extensive root networks can more effectively stabilize stream banks (Abernethy and Rutherfurd 2001, Pollen et al. 2004, Pollen and Simon 2005).

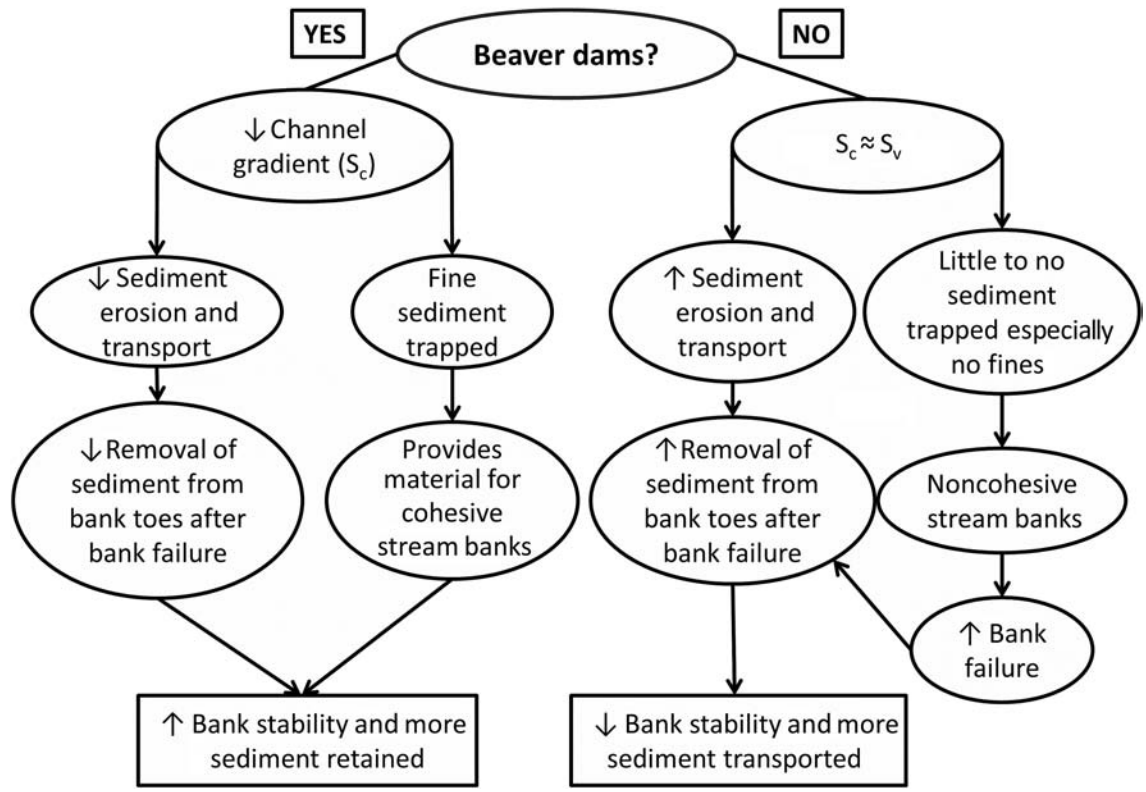

Figure 1. Flow diagram illustrating the long-term effects of the presence or absence of beaver dams on bank stability and whether sediment is retained or transported out of the system. With beaver dams, the local channel gradient (S_c) decreases, causing fine sediment to be trapped, and a decrease in stream power reduces transport. Beaver dams encourage the deposition of fine sediment not only in dams but also across the floodplain because of increased overbank flows and hydraulically rough vegetated floodplains. Fine sediment creates cohesive stream banks after the channel has migrated into the aggraded pond sediment, cohesive stream banks reduce the likelihood of bank failures' providing sediment to the bank toe, and the lower stream power reduces the removal of sediment from bank toes after bank failure. Without beaver dams, stream power varies approximately with the valley gradient (S_v); little to no sediment is trapped, especially no fine sediment. Fine sediment is not available to build cohesive stream banks, leading to more bank failures. Stream power is also higher, so bank toe is removed quickly.

As was discussed above, channels are able to form meanders with the addition of cohesion from vegetation, and studies of channel change after the invasion of exotic species indicate that different species can have differing effects on stream-bank stability. However, few studies have been focused on classifying or grouping species on the basis of stabilizing abilities (Norris et al. 2008, Evette et al. 2011). Stream-bank vegetation in the CFR can be categorized on the basis of its ability to provide added strength to the stream bank. Rhizomatous shrubs (commonly riparian) and trees provide more strength than xeric trees or nonrhizomatous graminoids and herbs, with the magnitude of the effect dependent on the bank texture and hydrologic conditions (Polvi 2011).

With these empirical field and modeling results on the contribution of vegetation to stream-bank stability as a starting point (Polvi 2011), we hypothesize that rhizomatous shrubs (e.g., willows) and graminoids (e.g., rushes), typically found in riparian zones, add more cohesion to stream banks than does most xeric vegetation (e.g., pines and spruces) and therefore encourage stream meandering in an originally braided system. The lower added cohesion and density of nonriparian species (e.g., conifers and other nonrhizomatous shrubs) are not sufficient either to cause a channel to cross the threshold from a braided to a meandering planform or to create lateral instability in an already-meandering channel. In a long-term perspective, on the order of 100–1000 years, during the transition from a braided to an anabranching channel system, beavers require a channel network that is less laterally mobile than a braided system, and certain vegetation types serve to assist in planform adjustment to a meandering system. With the establishment of a beaver-meadow complex, a sustained higher water table will favor riparian species, which, apart from being preferred food for beavers (Rosell et al. 2005), tend to be rhizomatous and maintain bank stability. Without reinforced stream banks, beaver-dam-induced overbank flows would be more likely to create relatively uniform erosion and deposition across the floodplain, rather than channel avulsions.

In logjam complexes, stream-bank vegetation is dominated by conifers that, overall, do not contribute substantially to stream-bank stability but do influence bank configuration through the existence of strong taproots and the addition of large wood that can either deflect the current toward the bank or protect the bank from erosion, depending on the orientation of the wood. Overbank flows initiated by logjams can easily cause scalloping of the stream bank and sediment entrainment between large conifers, which helps form additional channels.

Postglacial stream planform changes

By explicitly including the effects of biotic drivers of vegetation type and channel-spanning obstructions in the form of beaver dams and logjams, we can expand commonly used channel classifications that focus on the external driving factors of imposed valley gradient, sediment supply and size, and flow variables (e.g., Schumm 1977, Church 1992). Long-term planform changes should occur under predictable successional changes in vegetation and under long-term prevalence of channel-spanning obstructions. The abundance and type of stream-bank vegetation will affect the short-term bank stability conditions and the potential for a long-term sustainable beaver population and wood recruitment. Assuming a snowmelt-dominated flow regime in a gravel-bed channel system, distinct planform types are identified on the basis of the presence or absence of channel-spanning obstructions, which in turn depend on beaver populations or wood recruitment and in-stream wood loads and on the type of stream-bank vegetation (figure 2). Because channel-spanning obstructions can have long-term effects on floodplain sedimentation dynamics, planform may also represent legacy effects after the removal of the channel-spanning obstructions through natural or human disturbances. Therefore, planform in this classification should not be interpreted as a simple reflection of current conditions but as an integration of the effects of current biotic conditions with impacts from the valley's long-term planform history.

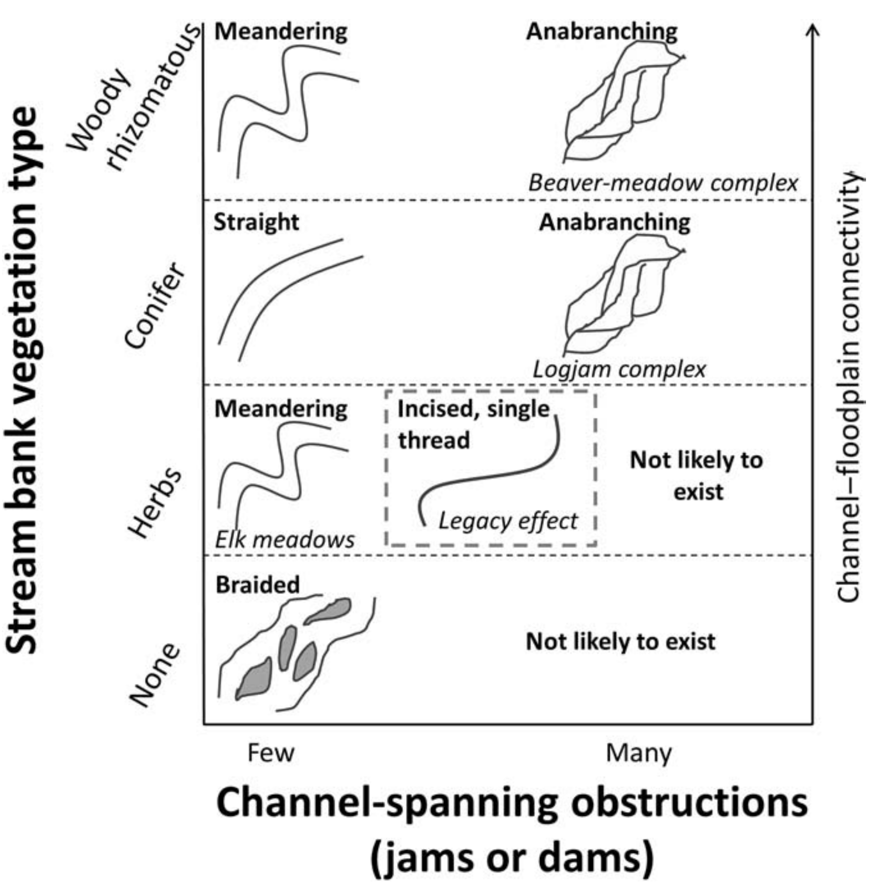

Figure 2. Conceptual diagram of probable long-term planform regimes in low-gradient, unconfined headwater valleys of the Colorado Rocky Mountains based on beaver populations and types of stream-bank vegetation. Legacy-effect planform is shown in a dashed box; planform occurs after long-term biotic channel-spanning obstructions have been removed from the system.

With no or very little stream-bank vegetation and few to no channel-spanning obstructions, we expect a braided channel to form. This dynamic system would hinder beavers from establishing even with a proper food source, and there is little wood recruitment to form logjams. With forbs and graminoids, the system could stabilize the stream banks to form a meandering channel. A meandering channel would remain with the addition of rhizomatous shrubs and trees. If, instead, conifers establish along the stream bank, a straighter channel forms because the conifers armor the stream banks with larger taproots. If channel-spanning obstructions are allowed to persist, an anabranching channel system will form. Long-term prevalence of channel-spanning obstructions alters the overall composition of floodplain material to include finer and, therefore, more cohesive material. A legacy effect of beaver removal, which is accompanied by a higher gradient (and therefore higher stream power) and by a lowered water table (and therefore more xeric vegetation), is a narrow, incised channel.

Following deglaciation, streams in broad, low-gradient valleys in the CFR have adhered to a path in planform evolution predictable from the establishment of vegetation, which allowed for the appropriate conditions for the

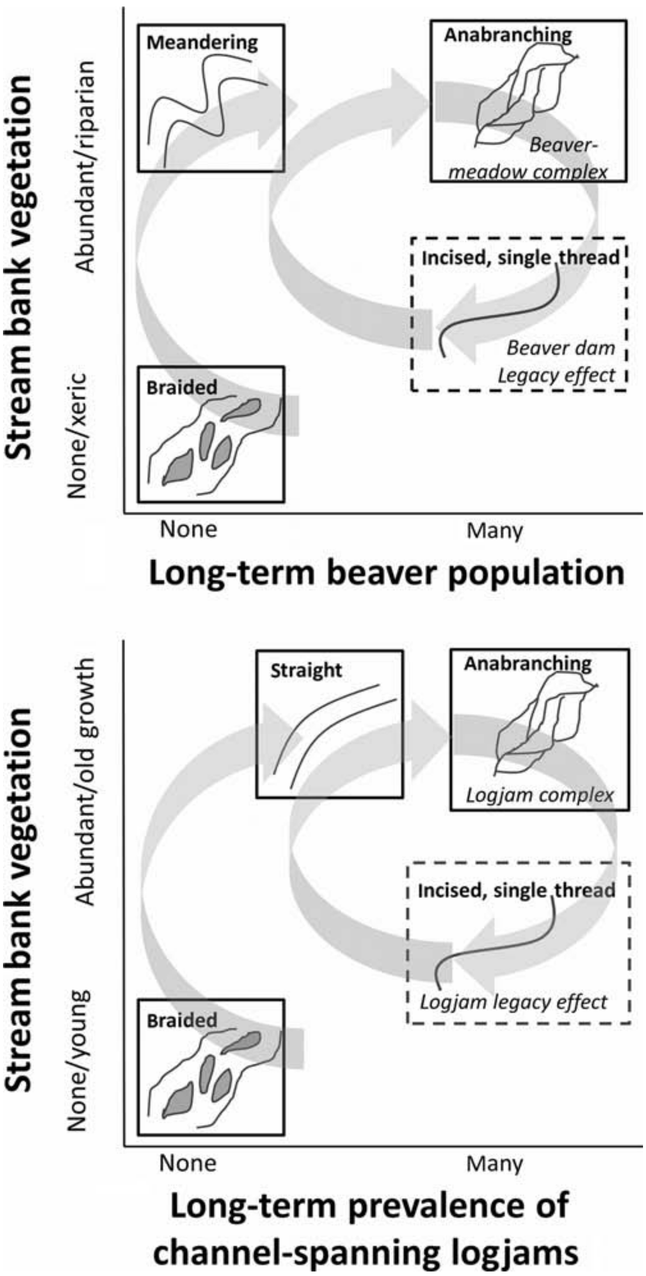

Figure 3. Conceptual diagrams of channel planform with different scenarios of stream-bank vegetation and biotic influences causing channel-spanning obstructions. The arrows show the likely direction of planform change and thresholds formed after channel-spanning obstructions have changed in-channel and stream-bank sediment dynamics. Planforms with a large long-term beaver population may represent a legacy condition from beavers shortly after the population has been reduced (the upper dashed box). A legacy planform is also possible in logjam valleys of an incised, single-thread channel (the lower dashed box) if sufficient fine sediment accumulated behind logjams and then the logjams were removed.

subsequent formation of channel-spanning obstructions (figures 3 and 4). Abundant riparian vegetation must be established before beavers can occupy a stream segment, and once beaver dams are constructed, overbank flows maintain higher water tables and the associated riparian vegetation. Contemporary studies have shown that beavers will establish and build dams in alluvial channels on the basis of two conditions: that there is a sufficient available food source of species such as aspen, willow, and alder (Gurnell 1998) and that the channel is under a threshold stream power governed by gradient and streamflow, which is highly correlated with channel size (McComb et al. 1990, Gurnell 1998, Persico and Meyer 2009). Riparian vegetation, which acts to stabilize stream banks, is necessary for beavers to become established for both of the reasons stated above: to supply a food source and to reduce the channel gradient by increasing the channel sinuosity by causing meandering. After beavers have been established in a valley for a sufficiently long period for fine sediment to be trapped (figure 1), the potential planform evolution is constrained to retaining an anabranching form or to becoming a single-thread, incising channel if beavers are removed. Although returning to the anabranching system is possible with the reintroduction of beavers and riparian vegetation, the system may have crossed over into an alternative ecohydrologic stable state. A lowered water table will preclude hydrophilic species, such as aspen or willow—a necessary food source for beavers. Although the magnitude of fine sediment necessary to cause a unidirectional threshold is unknown, the threshold can be defined when channel incision is greater than bank erosion and, therefore, greater than the lateral migration of the channel.

Threshold conditions exist between planforms, and planform reversal may be more difficult to initiate than the original planform evolution. Ratcheting conditions exist with vegetation for channel planform, as was noted by Tal and Paola (2007), and similar conditions occur in long-term planform change with the presence of beavers and riparian vegetation. In valleys with old-growth forests and logjam complexes, the effect is not as pronounced, because trapped sediment is coarser and thinner in depth, and narrower valley widths do not promote as extensive lateral channel migration. A new geomorphically stable planform develops with long-term beaver inhabitance of a valley, such that abundant fine sediment is trapped, rendering certain channel planforms impossible without extensive excavation and channel engineering. Either an anabranching channel planform is maintained with beavers, or a single-thread, incised channel will form in the absence of beavers. An ecological alternative stable state, in terms of vegetation abundance, diversity, and community composition, as well as the associated stream–land subsidies and faunal communities, follows the change in planform. A significant disturbance or hydroclimatic shift is necessary to move the system into the previous geomorphic and ecologically dynamic stable state.

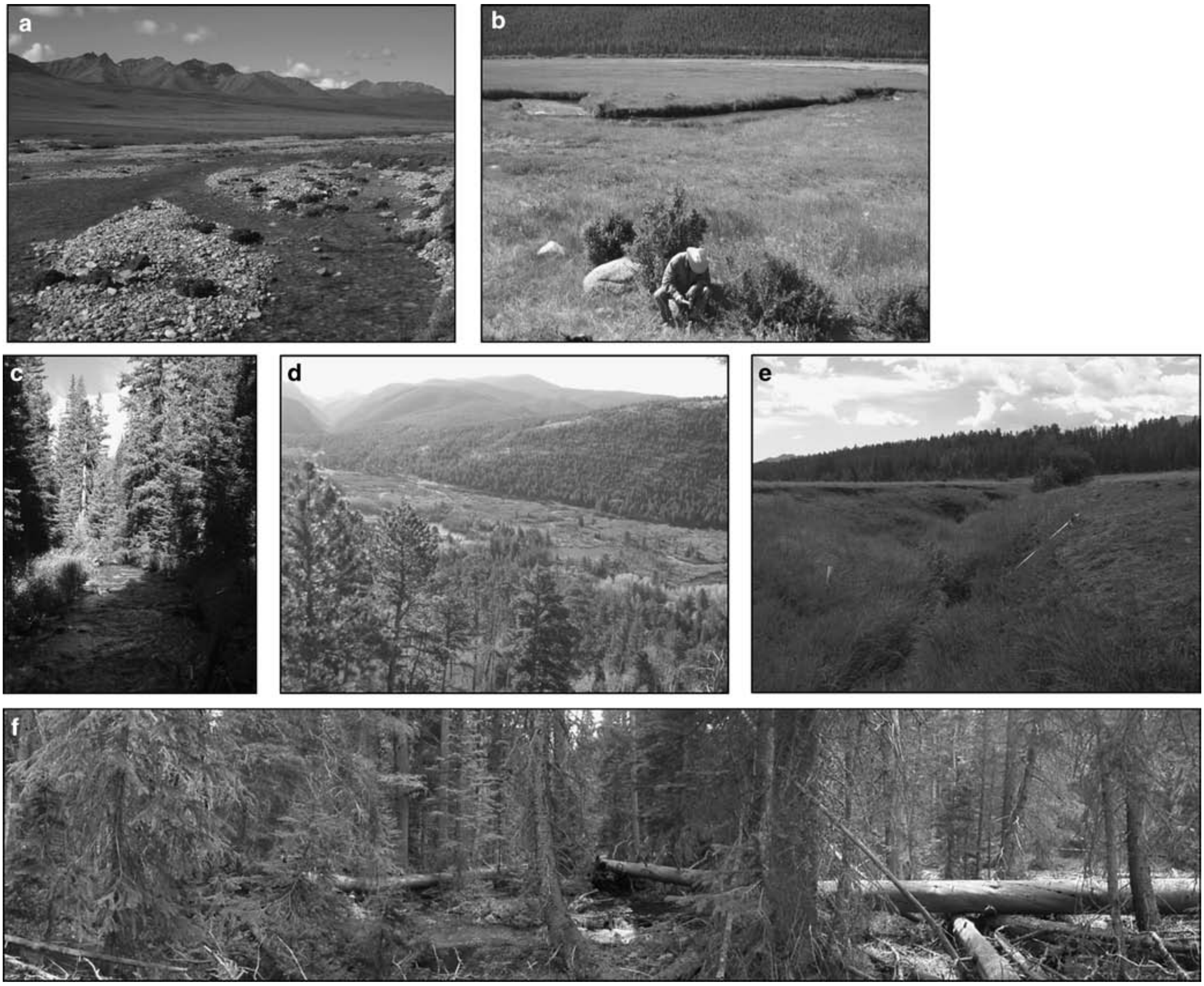

Figure 4. Various stages of planform development in the Colorado Front Range for valleys with long-term beaver populations and those with channel-spanning logjam complexes. (a) A braided stream is a dynamic system without abundant vegetation or channel-spanning obstructions (the photograph was taken at Brooks Range, Alaska). (b) A meandering stream forms with riparian vegetation to stabilize banks but without many dams or jams. (c) A straight channel forms in conifer forest without dams or jams. (d) Anabranching channels in a beaver-meadow complex. (e) An incised, single-thread channel forms after beavers are removed from the system. (f) Anabranching channels in a fully developed logjam complex. Photographs: Ellen Wohl (a, d) and Lina E. Polvi (b, c, e, f).

A similar path is followed for logjam valleys, with two distinctions. First, a straight channel is more likely to form after conifers establish. There may be a short transition phase of a meandering channel when young, early-seral species colonize the edges of the braided channel. Second, because logjams are typically leakier than beaver dams and allow continuous flow, the backwater area will be smaller than beaver ponds, which causes coarser and smaller amounts of sediment to be trapped (Wohl et al. 2012). Therefore, some incision is expected with the removal of logjams but not as much as when beaver dams are removed. Following the removal of in-stream wood, the system can more easily revert to a straight, nonincising channel or to an anabranching planform. Natural disturbances can hasten the transition from a straight to an anabranching system, because wood recruitment increases after fires, windthrow, or insect infestations. After the increase in wood recruitment to the stream, recruitment decreases for more than a century while the forest returns to the predisturbance state (Wohl 2011a). In-stream wood loads probably never vanish, however, because of slow wood decay and the ability of existing in-stream wood and persistent jams to retain wood transported from upstream (Wohl 2011a). Human disturbances, on the contrary, not only cause tree mortality but commonly remove all wood from the stream and floodplain, increasing the recovery time by limiting the retention of subsequently recruited wood and pushing the system toward incision or straightening. Wohl and Beckman (2011) referred to these as *wood-rich* and *wood-poor* alternative stable states.

A specific planform regime can be inferred for individual broad, low-gradient valley segments within the CFR throughout the Holocence (figures 5 and 6). Regimes differ slightly between valleys with beaver dams and those with logjams. Planform in beaver-dam valleys is controlled by climate, which has a direct impact on the riparian water table along a given stream segment, and vegetation type—both of which influence beaver population. Soon after glaciation, a meandering channel would form following the stabilization of the flow regime and channel with the establishment of riparian vegetation. Given paleontological evidence of the presence of wood cutting and semiaquatic beavers in North America for the past 25 million years (Rybczynski, 2007), as well as ecological evidence of beavers' preferred habitat, which is consistent with that available in headwater streams in the CFR (McComb et al. 1990,

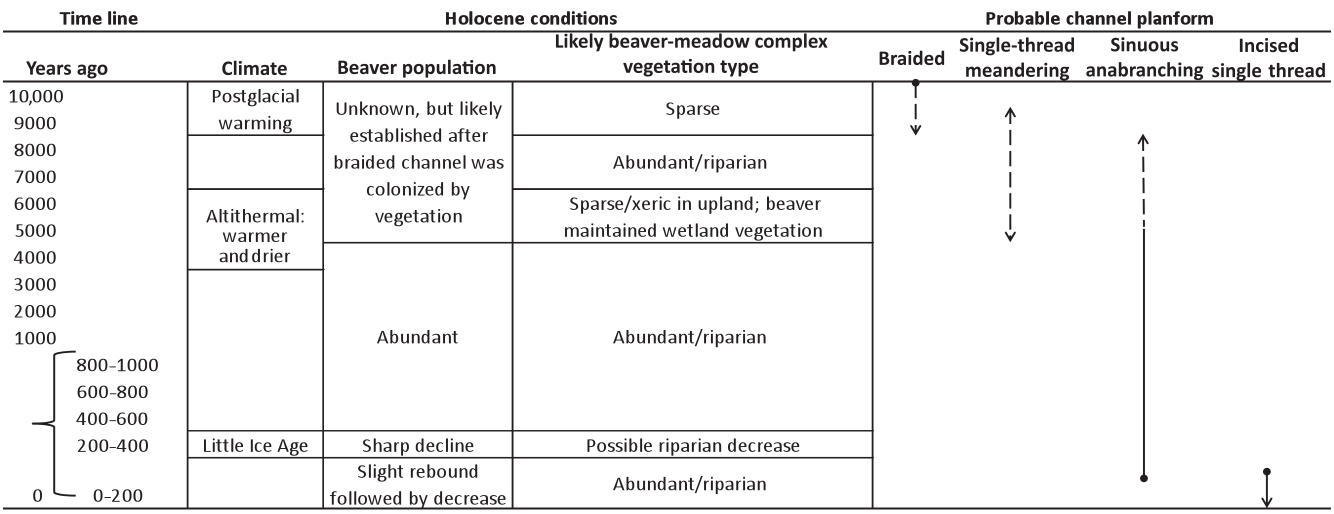

Figure 5. Inferred channel planform regime in unconfined, low-gradient headwater valleys with beaver populations based on Holocene conditions in the Colorado Front Range. Direct interpretations are not possible prior to 5000 years ago; therefore, several planform regime possibilities are given for this time period. For periods during which no climate range is given, the climate conditions are assumed to be comparable to contemporary conditions.

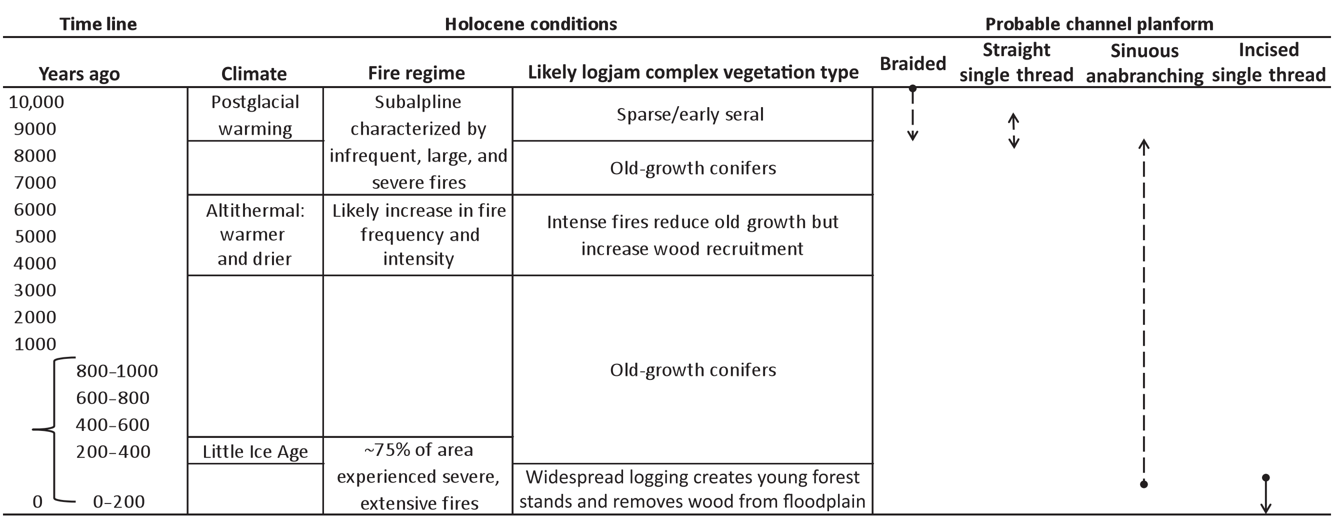

Figure 6. Inferred channel planform regime in unconfined, low-gradient headwater valleys with old-growth conifer forests based on Holocene conditions in the Colorado Front Range. Direct interpretations are not possible prior to 5000 years ago; therefore, several planform regime possibilities are given for this time period. For periods during which no climate range is given, the climate conditions are assumed to be comparable to contemporary conditions.

Gurnell 1998, Pollock et al. 2003, Persico and Meyer 2009), beavers most likely populated unconfined, low-gradient valleys in the southern Rockies relatively quickly after glacial retreat. With suitable habitat, beavers should be present in most stream networks throughout the Holocene. Necessary factors for beaver persistence are an ample food and building-material supply—*P. tremuloides* (aspen) and *Salix* spp. (willow) (Gurnell 1998)—and an appropriate stream morphology with low-gradient (less than 6%) alluvial channels, without coarse or bedrock substrates, and stream power below a threshold (McComb et al. 1990, Gurnell 1998, Pollock et al. 2003, Persico and Meyer 2009). Beaver establishment would be difficult on a braided channel because of the dynamic nature of sediment movement and channel change. There was probably a transition period, in which the stream changed into a single-thread, meandering channel with the aid of riparian vegetation, before beavers became established and an anabranching planform could develop.

A single-thread, bedload-dominated meandering channel would be expected to form if beaver populations did not establish, but rather, abundant bank-stabilizing vegetation took root. This planform regime is expected during periods in which beaver populations could not be sustained but when riparian vegetation was at least supported close to the main channel. Although beaver-related sediment was lacking in very small, northern Rocky Mountain valleys during the Altithermal period (6500–3500 years ago; Persico and Meyer 2009), beavers have been shown to mitigate drought conditions (Hood and Bayley 2008). Therefore, we hypothesize that beavers could have endured through the Altithermal period in small- to moderate-size streams in the CFR if an anabranching channel system were already established. With the raised water table and extensive riparian vegetation along the complex channel network, beavers could maintain a wet meadow complex and anabranching channels in broad valleys. Following an intense disturbance that reduces the riparian vegetation or beaver population, it would be much more difficult to return to this state than to simply maintain it, and the alternative stable state of a single-thread, partially incising channel would persist. The presence of beavers and their corresponding influence on stream planform after the postglacial warming (ca. 9000 years ago) through the Altithermal is very likely but not certain; however, evidence from the sedimentary record and near-surface geophysical imaging confirms the presence of beaver dams since at least circa 4000 years ago (Kramer et al. 2012, Polvi and Wohl 2012) and organic material–rich wetland mud and sand sediment since 5000 years ago (Madole 2012).

The final planform regime with sparse or xeric vegetation and abundant beavers is nearly impossible under natural conditions, because beaver populations cannot be sustained without riparian vegetation. Beaver trapping followed by outcompetition by ungulates in many valley segments of the study area has substantially decreased the beaver population. Channel adjustment from the changed biotic conditions caused the complex anabranching channel system to revert to a single-thread channel and the resulting excess stream power caused incision into cohesive bank sediment, creating an incised, single-thread channel, as has been observed in Rocky Mountain National Park (Polvi and Wohl 2012). The trophic cascade of increased elk browsing, which can outcompete beavers, thus reducing the beaver population and the number of beaver dams, after the removal of their main predator—wolves—can also cause the channel to revert to a more unstable braided system (Beschta and Ripple 2008, 2012). However, in the case study by Beschta and Ripple (2008) in Olympic National Park, Washington, there was no documented history of beaver damming to facilitate overbank deposition of a layer of cohesive bank material.

In logjam valleys, vegetation type, vegetation age, and the potential for wood recruitment are the main controls of planform, which are affected by climate and fire regime. In the case of beavers, large geomorphic or ecological disturbances, including ecological competition, disrupt beaver populations and can drive the system into a new planform type. Logjam valleys thrive on disturbance, because most natural disturbances provide a source of wood recruitment into streams, which allows the formation or reinforcement of current logjams. The subalpine zone is characterized by infrequent, large, stand-replacing fires, and wood recruitment into streams persists and even increases after a fire. Many of these fires will leave standing dead trees, which act as a wood source. However, large, stand-replacing fires do not severely affect the riparian zone. Blowdowns, such as those that occurred in the study area during the winter of 2011–2012, can directly influence riparian forests and add substantial volumes of wood to channels. Immediately post-glaciation, beads of low-gradient broad valley segments upstream of the terminal moraine were probably braided channel segments with large amounts of glacial outwash sediment and glacial meltwater. A straight single-thread channel probably formed within 1000 years of deglaciation, with the establishment of early-seral species, followed by conifer forests. An anabranching system would form as soon as an old-growth forest was established (after more than 200 years) and logjams formed and persisted over multiple snowmelt seasons, during which the logjams enhanced overbank flows. There is no reason to suspect that these valleys deviated from an anabranching system before widespread logging and tie drives caused wood removal in streams and wood storage on the floodplain, as well as the elimination of old-growth forest (Wohl 2001). Although we see evidence that gap-creating disturbances can result in local aspen colonization and limited beaver colonization of broader valley segments within old-growth conifer forest, these seem to be relatively temporary conditions (lasting less than 100 years), perhaps because of insufficient food to support large beaver colonies. Widespread human disturbance that removes old-growth forest and in-stream wood has largely ceased in the protected portions of the CFR during the past century, but two centuries are required for the establishment of old-growth forests and the associated larger-diameter trees and greater recruitment of in-stream wood that can sustain logjams and force anabranching.

Restoration and management implications

Anabranching channels provide many services that are considered desirable by managers and restorationists in maintaining a healthy and diverse ecosystem (table 1). Increased hydrologic channel–floodplain connectivity during high flows affects several geomorphic and ecological factors. Geomorphic effects of anabranching channels are driven by overbank flows, which drive altered rates of avulsions and sedimentation, causing channel change and changes in bank stability. The corresponding ecological effects are also driven by an altered overbank flow regime and by disturbances. In-channel and floodplain sedimentation enhance the deposition and retention of fine organic matter and carbon, which has been shown to be greater in valleys with beaver dams or logjams (Wohl et al. 2012). Avulsions are the primary mechanism for channel change in anabranching channel systems, which causes an increase in geomorphic complexity and habitat diversity and adds channel length for a given valley length. Ecological disturbance regimes differ in anabranching channel systems and meandering single-thread channels. Higher-energy flows will be more prevalent in a single-thread channel system within the channel and during overbank flows. The flows in an anabranching system are more variable and of lower energy, but overbank flows occur more often and affect a greater area. In-channel disturbances vary in the two systems. Increased bank stability and lower shear stresses in anabranching systems equate to greater stream-bank disturbances along single-thread channels. Beaver-dam building causes disturbance through altered in-stream habitat but increases the overall heterogeneity and complexity of the system (Naiman et al. 1988, Pollock et al. 2003, Rosell et al. 2005).

Ecological communities and nutrient cycling are indirectly affected by increased geomorphic complexity and increased overbank flow frequency. Riparian-zone width increases with anabranching channels, both because of an increased channel length and because of increased pond (or backwater with logjams) area and overbank flow frequency and magnitude. Geomorphic complexity enhances riparian biodiversity in beaver-meadow complexes and in logjam valleys by promoting hyporheic exchange and the presence of springhead channels with different water chemistry and nutrient dynamics than the main channel and by promoting greater diversity of soil textures and moisture levels. Because of their ecological importance and potential for nutrient storage, channel planform dynamics in unconfined valley segments have broad significance and implications for restoration practices.

In the restoration and management of fluvial environments with the goal of a dynamic, self-sustaining system and

Table 1. Comparison of in-channel and floodplain physical and ecological parameters for meandering single-thread channels and stable multithread channels with beaver dams and riparian vegetation.

Processes and characteristics	Meandering single-thread channel	Stable anabranching channel system with biotic channel-spanning obstructions
Overbank flows	Overbank flows occur less often and to lesser degree	Overbank flows occur more often, for longer duration, and with larger magnitude
Avulsions	Avulsions occur rarely; secondary avulsions may occur during extreme overbank flows	Avulsions are the main mechanism for channel change; primary and secondary avulsions occur with new dam construction and during overbank flows
Channel migration	Channel migration is the main mechanism for channel change; less cohesive sediment and less stabilizing vegetation create a dynamic environment	Channel migration is the secondary mechanism for channel change; it occurs at a rate similar to that of a single-thread channel
Sedimentation	Most or all sedimentation is on the floodplain during overbank flows or in-channel sedimentation preserved after channel migration; the long-term rates are constant; high transport rates are out of reach	There is more sediment deposited in the channel behind beaver dams and an increase in fine sediment deposited in the floodplain as a result of more frequent overbank flows; sedimentation is heterogeneous
Disturbance type	There are higher energy flows through the channel and during overbank flows	There are lower energy flows, but overbank flows affect a larger area and saturate the ground
Riparian zone	The zone forms along a narrow corridor, parallel to the channel	The riparian zone extends across the valley, past the channel closest to valley edge; a higher water table across the valley supports riparian vegetation
Vegetation type	Xeric vegetation is able to grow closer to the channel, because the floodplain is not often occupied by overbank flows; there is a mix of riparian trees and shrubs in the low-lying areas and upland species along stream banks	The wetter environment promotes growth of riparian shrubs and graminoids
Bank stability	There is more noncohesive sediment; riparian trees provide high local stability	Fine sediment increases bank cohesion; a mix of riparian shrubs and graminoids increases bank stability

Note: These effects are focused on headwater valleys with a snowmelt-dominated flow regime.

healthy ecosystems, efforts should be focused on restoration of the master variable of channel planform rather than on individual geomorphic and ecologic parameters (table 1). Insight into the long-term variability of channel planform provides managers with a tool to determine a restoration target state that bridges the gap between purely process-based modeling, which would require a complete understanding of all physical–biotic interaction, and using a reference condition, whether from a previous point in time or another location. We infer that in the CFR, anabranching channel systems in beaver-dam valleys have been present for at least the latter half of the Holocene, and logjam complexes have occupied other valley segments for the majority of the Holocene (figures 5 and 6), which had hydroclimatic conditions relatively similar to those of the present. This strongly suggests that the natural condition of these valleys, without human impacts, is a complex, multithread system with interacting biotic factors shaping geomorphic channel form. In addition, historical range of variability reconstructions can provide an important point of data that process-based modeling or reference conditions cannot: sediment legacy effects. Sediment legacy effects need to be accounted for to determine possible future planform in the absence of major reconstruction of the floodplain. Forced planform change through engineering measures may not be successful if the long-term biotic factors controlling planform are not taken into account. Long-term biotic factors may cause increased vertical incision rather than the desired lateral instability necessary for lateral migration in a meandering or anabranching system.

Thresholds between planform transitions, where reverting from an anabranching to a single-thread channel is difficult because of the legacy effects of fine sediment accumulation, create alternative ecohydrological stable states, in which the ratio of incision to lateral erosion is altered. In a meandering or anabranching channel system, the ratio is less than 1, whereas when the system has crossed a threshold after the removal of channel-spanning obstructions where abundant cohesive, fine sediment is present, the ratio becomes greater than 1. The magnitude of fine sediment necessary to change this ratio will vary depending on stream power and channel geometry. To return to a braided or single-thread, meandering channel in the absence of the ecological engineering effects of beavers, a hydroclimatic shift would be necessary for increased flows to rework the fine legacy sediment. This is unlikely, given the predictions that climate change will reduce snowmelt-driven flows in this region. Management and potential restoration of these systems are therefore limited to either a heavily engineered system with invasive techniques involving large amounts of fine sediment removal or a long-term plan of maintaining an existing anabranching system. Maintaining an anabranching channel requires protection of old-growth forest and beaver populations. In the absence of these biotic factors, channel planform change could be facilitated by creating a template suitable for beaver reintroduction, which would at first require artificial ponding to raise the water table and provide suitable conditions for beavers and their food source or the use of engineered logjams to mimic the effect of natural logjams.

Conclusions

We have added an integrated biomorphodynamic aspect to the understanding of channel planform and floodplain evolution, incorporating the interacting effects of several variables—stream-bank vegetation type and the presence of beaver dams or logjams—in determining channel planform. Channel planform has traditionally been viewed as a function of stream power, sediment supply, and substrate (e.g., Schumm 1977). Without any biotic controls, most broad low-gradient valleys would oscillate between a braided and a meandering system, according to the early classifications. A certain amount of stream-bank cohesion, such as that created by vegetation (e.g., Tal and Paola 2007) or cohesive finer sediment or bedrock (Leopold et al. 1964, Bhattacharya et al. 2005), is necessary for the formation of meandering channels. The formation of relatively stable anabranching channels, rather than more dynamic braided systems, in semiarid headwater valleys requires the interaction of several biotic controls. In the absence of channel-spanning obstructions, such as beavers or logjams, and riparian vegetation, the flow and sediment regimes in combination with valley geometry and substrate will determine channel and floodplain processes, which will most likely form only single-thread channels. The formation of relatively stable multithread channels has wide-ranging implications for geomorphic and ecological process and form (table 1). The physical and hydrologic processes of overbank flows, avulsions, and channel migration affect sedimentation patterns and riparian zone width and vegetation type, which influence bank stability. Because bank stability influences channel migration rates, this is not a linear system, in that feedbacks and thresholds determine the direction and magnitude of planform change. The feedbacks and thresholds involved in these interactions among biota, channel processes, and channel planform reflect a dynamic, nonlinear system. The observations and conceptual models that we have presented here are not unique to the CFR. An extensive literature documents the effects of beaver dams and channel-spanning logjams on stream process and form in diverse environments. Interactions among Holocene climate and hydrologic change, vegetation communities, and stream dynamics can be inferred for a wide variety of headwater streams using the approach that we have presented.

Acknowledgments

Parts of this study were funded by the US Forest Service Stream Team and a Geological Society of America Graduate Student Research Grant (awarded to LEP). We thank Tim Beechie, David Strayer, and an anonymous reviewer for their constructive reviews that substantially improved the manuscript.

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