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The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development

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ABSTRACT: We evaluate the validity of the beaver-meadow complex hypothesis, used to explain the deposition of extensive fine sediment in broad, low-gradient valleys. Previous work establishes that beaver damming forms wet meadows with multi-thread channels and enhanced sediment storage, but the long-term geomorphic effects of beaver are unclear. We focus on two low-gradient broad valleys, Beaver Meadows and Moraine Park, in Rocky Mountain National Park (Colorado, USA). Both valleys experienced a dramatic decrease in beaver population in the past century and provide an ideal setting for determining whether contemporary geomorphic conditions and sedimentation are within the historical range of variability of valley bottom processes. We examine the geomorphic significance of beaver-pond sediment by determining the rates and types of sedimentation since the middle Holocene and the role of beaver in driving floodplain evolution through increased channel complexity and fine sediment deposition. Sediment analyses from cores and cutbanks indicate that 33–50% of the alluvial sediment in Beaver Meadows is ponded and 28–40% was deposited in-channel; in Moraine Park 32–41% is ponded sediment and 40–52% was deposited in-channel. Radiocarbon ages spanning 4300 years indicate long-term aggradation rates of ~0.05 cm yr^{-1}. The observed highly variable short-term rates indicate temporal heterogeneity in aggradation, which in turn reflects spatial heterogeneity in processes at any point in time. Channel complexity increases directly downstream of beaver dams. The increased complexity forms a positive feedback for beaver-induced sedimentation; the multi-thread channel increases potential channel length for further damming, which increases the potential area occupied by beaver ponds and the volume of fine sediment trapped. Channel complexity decreased significantly as surveyed beaver population decreased. Beaver Meadows and Moraine Park represent settings where beaver substantially influence post-glacial floodplain aggradation. These findings underscore the importance of understanding the historical range of variability of valley bottom processes, and implications for environmental restoration. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: floodplain; sedimentation; beaver; Holocene

Introduction

The beaver-meadow complex

Beaver (*Castor fiber* in Europe, *Castor canadensis* in North America) are large rodents that build low dams of sediment and wood across stream channels. Although beaver can occupy most portions of a forested stream network, the animals prefer unconfined, low-gradient (<6%) alluvial channels, without coarse or bedrock substrates, and below a stream power threshold (McComb *et al.*, 1990; Gurnell, 1998; Pollock *et al.*, 2003; Persico and Meyer, 2009). Woody vegetation is a necessary food source, including willow, alder, and maple, but with a strong preference for aspen (Gurnell, 1998), which tend to thrive in the wet floodplains created by beaver (Rosell *et al.*, 2005).

Beaver are considered ecosystem engineers and their ecological importance is well documented in numerous studies across a range of forested, temperate environments (Naiman *et al.*, 1986, 1988; Wright *et al.*, 2002; Rosell *et al.*, 2005). Their long-term geomorphic significance is less well established. Studies of contemporary beaver dams indicate that beaver activity can alter channel longitudinal profiles, create localized sediment storage in backwater ponds, cause high magnitudes of sediment transport during potentially catastrophic dam failures (Butler and Malanson, 1995; Gurnell, 1998; Pollock *et al.*, 2003, 2007), and increase extent and duration of overbank flooding and associated alluvial groundwater recharge (Westbrook *et al.*, 2006). Beaver dams can increase the potential for channel avulsions (John and Klein, 2004); this has been suggested to cause a multi-thread channel network downstream of the dam (Woo and Waddington, 1990; Burchsted *et al.*, 2010). While a beaver dam is active, rates of sediment aggradation behind dams exceed those in adjacent undammed segments of the stream and floodplain (Butler and Malanson, 1995). The relative importance of beaver-induced geomorphic changes over hundreds to thousands of years, however, remains uncertain.

The term 'beaver-meadow complex' grew out of work during the first half of the 20th century and refers to wet meadows with multi-thread channels that occur in broad, low-gradient valleys as a result of beaver dams; it has been proposed as a mechanism for accumulating significant magnitudes of sediment in broad, low-gradient valleys in headwater segments (Ruedemann and Schoonmaker, 1938; Ives, 1942; Rutten, 1967). In broad, low-gradient valleys with a glacial legacy, these workers suggested beaver as the cause for accumulation of fine sediment rather than the previous explanations of channel meandering (Ruedemann and Schoonmaker, 1938), silted up glacial lakes (Ives, 1942), or deposition from braided channels (Rutten, 1967). Ives (1942), who worked in northern Colorado, observed that beaver pond deposits are not spatially extensive, suggesting spatially and temporally variable deposition, which is in contrast to a filled glacial lake. These studies of the beaver-meadow complex are largely inferential and lack systematic data collection of geomorphic forms or volumes of sediment resulting from different depositional processes.

There has been little quantitative evaluation of the hypothesized beaver-meadow complex until recently. In addition, the importance of beaver aggradation relative to other alluviation processes has not been quantified for glacial troughs, the wide, low-gradient valley segments that store the largest volume of sediment in glaciated, mountainous river networks (Wohl, 2010). Several studies demonstrating the efficiency of current beaver ponds in trapping sediment (Butler and Malanson, 1995; Meentemeyer and Butler, 1999; Bigler *et al.*, 2001) support the central role accorded to beaver dams in the beaver-meadow complex hypothesis. Persico and Meyer (2009), however, noted only minor effects of beaver aggradation in a study in Yellowstone National Park through multiple valleys segments. In most reaches, beaver-induced aggradation was <2 m; however, in low-gradient reaches, vertical stacking of ponded sediment was observed (Persico and Meyer, 2009). To evaluate the overall long-term significance of beaver-ponded sediment in broad, low-gradient valleys, which are the sediment storage centers within headwater reaches, knowledge of the subsurface sediment geometry is necessary. If relatively shallow post-glacial alluvium overlies thicker glacial deposits, then even a few meters of patchy, beaver-induced sedimentation can constitute a significant percentage of this alluvium.

In this study, we examine whether beaver-pond sediment can have a major influence on fluvial sedimentary and geomorphic character even without accumulating to large thicknesses. We focus on low-gradient glacially-carved valleys that might be expected to store sediment and organic matter even in the absence of beavers, and quantify the proportion of total post-glacial alluvium associated with beaver ponds. Beaver dams facilitate formation of spatially heterogeneous sediment patches over time from cycles of beaver colonization and abandonment (Westbrook *et al.*, 2011), and can potentially result in substantial sediment contributions in some geomorphic settings. We focus on valley bottom processes that trap sediment in broad, low-gradient valleys in the southern Rocky Mountains of Colorado, USA.

Importance of historic range of variability

Low-gradient, unconfined headwater valleys present an ideal location to study alluvial processes and the historical range of variability of geomorphic processes in valley bottom sedimentation. Mountainous headwaters tend to act as sediment sources (Schumm, 1977; Milliman and Syvitski, 1992), with relatively minor sediment storage relative to lowland portions of a drainage basin. Mountainous headwaters also display substantial longitudinal variability in valley geometry, however, with limited wider, lower gradient portions of the river network that are capable of substantial sediment storage (Wohl, 2000, 2010). Glacial processes have played a large role in creating the geomorphic forms able to store sediment, including glacial troughs, moraine-bounded valleys, overdeepened valleys, and stepped valleys.

In the context of this study, we define historical as encompassing the period between ~4000 years ago and the initial exploration of the region by people of European descent during the first decade of the 19th century. We choose this time period because we have sediment and aggradation data up until ~4000 years BP and the climate has been relatively stable since the end of the Altithermal that ended ~3500 years BP (Short, 1985; Elias *et al.*, 1986; Elias, 1996). Although conditions may have been similar during the early-mid Holocene and therefore valley bottom processes could be extrapolated, our data only extend for the past 4000 years. Many of the valley bottoms in the Colorado Rockies have been extensively altered by diverse land uses during the past two centuries. Characterizing historical range of variability of valley bottom processes, as related to sedimentation type, rate, and magnitude for these landscapes becomes particularly important as resource managers seek to restore riparian ecosystems.

The magnitude, type, and rate of post-glacial sedimentation resulting from beaver activity likely reflect Holocene hydrology and sediment yield, which in turn are a function of climate, vegetation and hillslope processes. All of these parameters varied during the Holocene (Woodhouse, 2001; Shuman *et al.*, 2009). Beaver populations and dam-induced sedimentation and multi-thread channels also presumably varied during the Holocene, creating some range of historical variability prior to when fur trappers began removing beaver from the study area during the first decade of the 19th century. With the reduction of beaver populations, the beaver-meadow complex changes and may lose significance in valley or channel development. Without beaver, geomorphic and ecologic systems can change to an alternative stable state that is fundamentally outside of the range of historic variability (Sutherland, 1974). For river and ecosystem restoration, the trajectory of the current and past valley formation determines the available habitat template and possibilities for geomorphic process. Natural range of variability ecosystem management is based on the concept that past processes provide context for management of ecological systems and that disturbance-driven heterogeneity is an important ecosystem attribute (Landres *et al.*, 1999). Therefore, an understanding of historical, natural patterns of sedimentation and channel complexity can be used as a model of how ecological and geomorphic systems have evolved together (Veblen and Donnegan, 2005).

Objectives

Sediments deposited in valley bottoms record watershed-scale landscape processes through sediment storage and removal over varying timescales. By examining valley bottom sediment, we can examine: (1) the range of variability in sedimentation rates and types since deglaciation, (2) the relative importance of fluvial processes, e.g. flooding and lateral channel movement, compared to hillslope processes, e.g. mass movements or wildfires, in floodplain sedimentation, (3) the role of beavers in driving floodplain evolution, and spatial and temporal discontinuities in sedimentation, and (4) whether beaver dams alter channel complexity and promote greater magnitudes of sedimentation throughout a valley. Examining these issues allows us to determine the chronology and processes of post-glacial alluviation. By inferring the relative importance of these processes, we can understand post-glacial landscape processes and the historical range of variability in the Rocky Mountains and make management recommendations regarding the relative importance of beavers in creating particular geomorphic conditions. Additionally, we can revisit the beaver-meadow complex hypothesis and determine whether beaver have fundamentally changed processes in post-glacial alluviation by altering sedimentation or channel form.

Study Area

We focused on two glacially formed valleys on the eastern side of the Continental Divide in Rocky Mountain National Park (RMNP): Moraine Park and Beaver Meadows (Figure 1), located along the Colorado Front Range at approximately 2440 m elevation. Several cycles of alpine glaciation are recorded in the southern Rocky Mountains. Pre-Bull Lake glaciation, extending from 1800 to 300 ka, incorporates several glacial maxima without clear signatures on today's landscape (Richmond, 1960; Chadwick *et al.*, 1997). Bull Lake glaciation occurred from 300–130 ka; Pinedale glaciation extended down to ~2300–2400 m elevation, lasted ~20 000 years, and ended 10–15 000 years ago, depending on elevation (Madole, 1980; Madole *et al.*, 1998). Because Moraine Park and Beaver Meadows are located within 1 km of the terminal moraine (Braddock and Cole, 1990; Madole *et al.*, 1998), we assume the study sites were deglaciated ~15 ka (Madole, 1976; Madole, 1980). Although there were significant gaps between glacial episodes, during which alluvial processes dominated in the study valleys, we focus on the sedimentation history after the end of the latest Pleistocene, Pinedale glaciation.

Moraine Park is bounded by two lateral moraines and was glaciated in the Pinedale as well as earlier. Moraine Park is approximately 3 km long and 1 km wide. The Big Thompson River, which flows through Moraine Park, is a pool–riffle stream with an active channel 8–15 m wide, and a bed gradient of ~1.5%. At the downstream end of Moraine Park, the Big Thompson River drains an area of 103 km^2, originating at the Continental Divide at 3600–4300 m. Beaver Meadows is bounded by one of Moraine Park's lateral moraines to the south and by granite, gneiss, and schist bedrock to the north (Braddock and Cole, 1990). Beaver Meadows is 2.5 km long and 75–300 m wide. Beaver Brook drains an area of 15 km^2, with a mean elevation of 2810 m. Beaver Brook is 0.2–1.5 m wide with a bed gradient of 0.2–0.8%. Beaver Meadows was glaciated during earlier episodes, but not during the Pinedale. The hydrographs of these streams located at ~2450 m elevation are dominated by snowmelt and high-magnitude floods are rare (Jarrett and Costa, 1988).The basins receive an average of ~680 mm yr^{-1} precipitation.

These valleys are located within the montane ecozone, with hillslope forests dominated by ponderosa pine (*Pinus ponderosa*) and to a lesser extent lodgepole pine (*P. contorta*). Vegetation in the valleys consists of xeric and mesic species. Because the channel in Beaver Meadows is incised (0.5–2 m) and the channel in Moraine Park is restricted to limited parts of the valley, the contemporary channel, overbank flooding, and the associated shallow alluvial aquifer likely do not have a large influence over vegetation in most of each valley. Xeric vegetation that has recently encroached on the valley bottoms includes small ponderosa pines, native and non-native thistles, graminoids and herbaceous species. The main mesic vegetation is water birch (*Betula occidentalis*) and gray alder (*Alnus incana*). Few to no willows (*Salix* spp.) are present in either valley, although historical ground photographs and descriptions suggest that they were present during the 20th century.

Forest fires in the montane zone were frequent but were mostly surface fires prior to 20th century fire suppression (Veblen *et al.*,

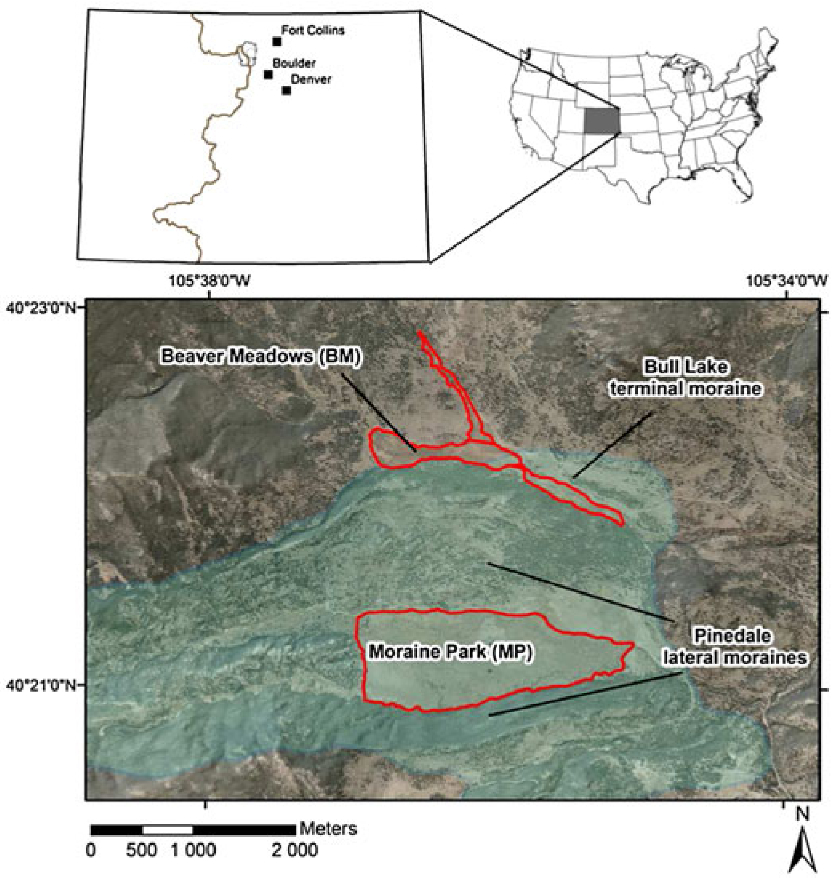

Figure 1. Location map of the two study valleys, Beaver Meadows and Moraine Park, in Rocky Mountain National Park (RMNP) in north-central Colorado. In the map of Colorado, the north–south line represents the Continental Divide, and the boundary of RMNP is shown; the two white circles represent the locations of the study valleys. The study valleys are shown on the 2001 aerial photograph with a hillshade DEM below; the shaded area represents the extent of glaciation (Madole *et al.*, 1998). Beaver Meadows is divided into the three segments as detailed by Kramer *et al.* (in review): East Beaver Meadows (EBM), bounded by glacial till to the north and south, West Beaver Meadows (WBM), bounded by glacial till to the south and bedrock to the north, and North Beaver Meadows (NBM), outside the range of glacial extent. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

2000). At the elevation of Beaver Meadows and Moraine Park, the fire regime transitions into the subalpine forest zone because ponderosa pine is intermixed with lodgepole pine and Douglas fir. The subalpine forests in RMNP are affected by infrequent but extensive stand-replacing fires (Brown *et al.*, 1999; Sibold *et al.*, 2006). This low fire frequency means that fire-induced sedimentation would also be infrequent; however, stand-replacing fires could be geomorphically effective with sediment pulses transported into low-gradient valley segments.

Regular surveys of beaver populations, or the proxies of beaver lodges, were conducted in RMNP throughout the 20th century. The beaver population in Moraine Park decreased drastically throughout the 20th century: 315 beaver were present in 1940, then the population dropped by 96% to only 12 in 1980 (Packard, 1947; Stevens and Christianson, 1980; Mitchell *et al.*, 1999). In 1999, only 6 beaver were present, and no beaver activity was observed during this study in the summers of 2009 and 2010. In Beaver Meadows, 36 beavers were surveyed in 1940 and by 1980 none were present. The dramatic decline in beaver has been attributed to competition with elk for willow, an important winter food source for beavers (Peinetti *et al.*, 2002; Baker *et al.*, 2005). Elk numbers increased following the removal of their main predator, the wolf, from the park by the start of the 20th century (Ripple and Beschta, 2003). Park managers have experimented with various elk-reduction strategies since the 1930s (Buchholtz, 1983). Packard (1947) noticed that Beaver Meadows and Moraine Park were already being overgrazed by elk and deer. Where beaver have been removed from valleys, an altered hydrologic state exists, which may not allow beaver to return the valleys to their original state by simply excluding elk and reintroducing willow (Westbrook *et al.*, 2006; Wolf *et al.*, 2007).

Although no paleontologic data on the Holocene history of beaver exist for RMNP, beavers are known to have been present throughout most of the contiguous United States until the arrival of European fur trappers (Naiman *et al.*, 1988). Wood-cutting, semi-aquatic mammals in the Castoridae family, of which *C. canadensis* and *C. fiber* are a part, evolved as early as 25 million years ago (Rybczynski, 2007). This suggests that beavers have cut trees and built dams, potentially altering riparian corridors and geomorphic process, at least through the Pleistocene. Therefore, beavers were likely present in RMNP whenever climatic and ecologic conditions allowed.

Supporting geophysical data

The overall subsurface sediment geometry in Beaver Meadows was described in detail using the shallow geophysical techniques of near-surface seismic refraction (SSR) and ground penetrating radar (Kramer, 2011; Kramer *et al.*, In press). In this study, Beaver Meadows was divided into three regions: East Beaver Meadows (EBM), which is bounded by glacial till to the north and south, West Beaver Meadows (WBM), which is bounded by bedrock to the north and till to the south, and North Beaver Meadows (NBM), which is the tributary valley that joins Beaver Meadows at the eastern end of WBM (Figure 1). Geophysical techniques were used to differentiate crystalline bedrock, glacial deposits, post-glacial alluvium, and beaver pond sediments. Mean total valley fill depth, which includes glacial deposits, post-glacial alluvium, and beaver pond sediments, was 16 m in EBM, 10 m in WBM, and 1.3 m in NBM. The maximum and mean alluvial thicknesses, which include all the post-glacial alluvium and beaver pond deposits, in EBM, WBM, and NBM are 2.5 and 0.7 m, 6.0 and 1.8 m, and 3.5 and 1.3 m, respectively (Kramer *et al.*, In press). From isopach maps, the percentage of alluvium in the valley fill was determined to be only 5% in EBM, 19% in WBM, and 100% in NBM. Using type facies from sediment beneath surface features interpreted as buried beaver dams, Kramer *et al.* (In press) estimated the percentage volume of alluvium attributed to beaver dams and ponds as 64% in EBM, 28% in WBM, and 38% in NBM.

In Moraine Park, SSR was used to determine the depth to bedrock, which ranges from 5–30 m (N. Kramer, unpublished data). The total volume of valley fill (glacial and alluvial fill) is approximately 24 million m^3, compared with 5.3 million m^3 in Beaver Meadows (including EBM, WBM, and NBM). When standardized for the valley area, however, the total valley fill is quite similar: 10.7 m^3/m^2 in Beaver Meadows and 12.6 m^3/m^2 in Moraine Park.

These data give us the template from which we can deduce the Holocene stratigraphy, aggradation chronology, and importance of beavers in aggradation. In evaluating the beaver-meadow complex hypothesis, we need to determine whether beavers played a significant role in sediment aggradation. Because the depth of alluvium is only ~2 m, then even a small magnitude of beaver-related sediment aggradation can be significant.

Methods

We used three primary lines of evidence in addition to near-surface geophysical data to evaluate the influence of beavers on post-glacial sediment accumulation at the study sites. We quantified sediment texture and age within 2 m of the surface at numerous locations in both study areas, we mapped contemporary landforms across each valley bottom, and we measured the extent of beaver ponds and channel planform on aerial photographs spanning several decades.

Sediment characterization and radiocarbon chronology

Because we worked in a public area of a national park, we used non-invasive methods to analyze near-surface sediment, defined as the sediment within 2 m of the surface. This sediment was accessible along cutbanks and in ~2 m-deep hand-augered cores. We recorded sediment texture, sorting and angularity, presence of organic material, such as wood, leaves or roots, color of sediment as an indicator of past anoxic or aerobic conditions, and depth of layers and type of boundary between each layer. The depth of the water table was also recorded. The auger reached a depth of ~1.9 m; cores ended at this depth, when impenetrable substrate was encountered or when too much infilling occurred, usually with a rounded, well-sorted sand below the water table. At the bottom of each core, we recorded the substrate encountered as similar to previous layer; coarse gravel to cobbles; or large cobbles, boulders, or bedrock. Using the auger, it is possible to feel whether the sediment moves but cannot be picked up (coarse gravel to cobbles) or is completely impenetrable (cobbles to bedrock). Descriptions of cutbanks included more detailed stratigraphy. In Beaver Meadows, the channel throughout most of the valley is incised up to 1–2 m, which allowed for detailed observations of stratigraphy including boundaries between layers not preserved within cores. Samples were taken of characteristic sediment types. We sieved sediment samples and used a hydrometer to determine the clay and silt fraction of the remaining sediment smaller than 4 φ (0.0625 mm). To interpret the depositional environment, we collected samples of modern sediment in known depositional environments, including the hillslope and the pools and riffles of the channel. Because there were no active beaver ponds or dams in either Beaver Meadows or Moraine Park, beaver pond sediment was collected from two proxy locations: (1) in Moraine Park, upstream of a minor berm, in what is interpreted to be an abandoned beaver pond that is currently a dried, marshy pond, 5–10 m from an active channel, and (2) in active beaver ponds along Corral Creek valley, located north of RMNP in the headwaters of the Cache la Poudre River, with channel and valley dimensions roughly between that of Beaver Meadows and Moraine Park. Samples of silt- and clay-rich sediment were analyzed for organic content by measuring mass before and after burning off all organic material.

We used radiocarbon dating to obtain dates of wood and charcoal samples, of which 16 were from Beaver Meadows and 3 from Moraine Park. Three cores had two samples dated from different depths (BM01 and BM02; BM09 and BM10; and BM11 and BM14) and a fourth core had two samples from approximately the same depth (BM03 and BM04). We used the weighted mean of the calibrated probability distribution of ages with 2σ ranges to obtain a single age for each dated sample that could be used to calculate aggradation rates (Telford *et al.*, 2004). Net, average aggradation rates were calculated by simply dividing the depth at which the sample was found by the age. Six organic samples of wood and charcoal were dated using the University of Arizona Radiocarbon Lab via standard analyses; 13 samples were dated by Beta Analytic Inc. using accelerator mass spectrometry.

Geomorphic mapping

Using a 2001 aerial photograph as a template, we mapped contemporary landforms in the field, including the active floodplain, hummocky landforms, glacial deposits, and ramps or berms in the valley profile perpendicular to the valley axis (Persico and Meyer, 2009), which we interpreted as abandoned beaver dams. Hummocks are raised surfaces, usually in fine-grained sediment, with abundant sedges, and ~0.2–0.5 m in height and 0.4–0.1 m in diameter. We surveyed the valley geometry with a total station to determine valley length and widths, channel sinuosity, and valley and channel gradient. Twelve valley cross-sections were surveyed in Beaver Meadows and the entire valley and channel longitudinal profiles were surveyed. Because of the large size of Moraine Park, it was divided into three study reaches, approximately 300 m long. For each reach, we surveyed a valley cross-section, and valley and channel longitudinal profiles.

In Moraine Park, evidence of beaver influence is still prevalent in the form of abandoned beaver dams and beaver-chewed wood deposited in the channel. We walked the entirety of the main channel and all of the side channels in Moraine Park and noted any occurrences of abandoned beaver dams, beaver-chewed wood, or instream wood without evidence of beaver influence. Structures with clearly beaver-chewed wood that were tightly packed with other debris and sediment and attached to at least one streambank were identified as abandoned beaver dams. For each wood observation, the local in-channel geomorphic structure was recorded: channel splits and junctions; islands, which were smaller in width than the combined channel widths of the two side channels; a cutbank or point bar; or a sharp bend where the bend around a point bar was 90° or less.

Aerial photo analysis

We used historical aerial photographs to assess the historical presence of beaver dams or ponds and to quantify channel planform change. We obtained a series of aerial photographs of Beaver Meadows and Moraine Park from the late 1930s to 2001. In Beaver Meadows no historical beaver ponds or multi-thread channel systems were visible, except one other channel that was present for a brief time period. We were, however, able to identify linear features (perpendicular to the valley axis) with pond-like shapes, delineated by changes in vegetation, up-valley. In Moraine Park, multiple channels and ponds were historically abundant and apparently dynamic during the time of the aerial photo series. For the Moraine Park photos, we digitized ponds and calculated total area and number of ponds for each year of photographic coverage. We determined channel complexity in two ways: we digitized all the channels and calculated total channel length, and we calculated a braiding index (Bridge, 1993). The braiding index was determined by counting the number of stream channels that crossed 18 valley-wide transects, which were spaced ~250 m apart; the mean and standard deviations for each year were compared. The braiding index and total channel length were compared with trends in the number or area of ponds.

Results

Sediment textures at both sites were comparable, although larger grain sizes were found in Moraine Park. Grain sizes ranged from clay to coarse gravel in Beaver Meadow, and clay to small cobbles in Moraine Park. Most sand- to cobble-sized sediment was sub-rounded to well-rounded. Alternating layers of fluvial sands, gravels, and cobbles with layers of clay to fine sand were commonly seen in cutbanks and cores. Ten sediment texture categories were identified and used to classify sediment in cores and cutbanks; these include organic soil, fluvial sands and gravel, very fine grained sediment, and oxygenated and anoxic clays through gravel (Table I).

Interpretation of sediment depositional settings

Using modern analogs, we interpreted a range of possible depositional settings for each sediment category. Table II shows descriptions and results from textural analyses of in-channel sediment in Beaver Meadows and Moraine Park, hillslope sediment from Beaver Meadows, and beaver pond sediment from Moraine Park and Corral Creek. Channel sediment in Beaver Meadows is slightly smaller (very fine gravel) than that in Moraine Park (medium- very coarse gravel). Sediments in Beaver Meadows were sub-rounded to sub-angular; fluvial sediments within this valley do not necessarily show significant rounding because of the small drainage area. The in-channel sediment in Moraine Park was much more rounded than that of Beaver Meadows.

We interpret any very fine-grained sediment as being deposited in a pond behind a beaver dam. Other possible causes for fine-grained sediment were eliminated in these study areas. Log jams and debris flows could cause damming of water and sediment and thus deposition of fine-grained sediment. However, these broad valleys are relatively disconnected from the hillslopes, thus reducing wood recruitment into the channels. If any long-lasting instream wood is recruited, the low channel gradients (<1 %) limit transport and formation of a jam. Additionally, we have observed elsewhere in the river network that wood from deciduous riparian species that enter the channel (birch, alder, willows) disintegrates quickly and will not form jams. No contemporary of stratigraphic evidence of debris flows was observed, and hillslopes bordering the study reaches have low gradients and are fairly short, limiting mobilization of hillslope sediment by intense rain or snowmelt. Cutoffs or avulsions that could trap sediment are not evident, and interpretation of fine sediment as beaver pond sediment is supported by geophysical evidence of onlapping structures (Kramer *et al.*, In press).

Cores in Beaver Meadows showed characteristic sequences of alternating fluvial and ponded sediment, especially close to the channel and up-valley of any linear berms, which also usually coincided with hummocky surface features (Figure 2,

Table I. Sediment categories identified in Beaver Meadows and Moraine Park.

Abbr.	Layer name	Color	Texture	Macroscopic organics	Depositional environment
OS	Organic soil	Dark brown	Clay to fine sand	Abundant roots	Modern soil formation
CS	Very fine grained	Dark brown- black	Very fine grained; mostly clay and silt; possibly minor sand	Minimal to extensive	Pond behind beaver dam
CSS	Fine grained	Dark brown- black	Fine grained; Clay, silt, and fine sands	Minimal to extensive	Pond behind beaver dam
CSG	Clay to fine gravel	Light- dark brown	Clays, silt, sand & gravel; sands and gravels are subrounded- subangular	Minimal to none	Pond or overbank
CSG+O	Oxygenated clay through gravel	Light- dark brown & red/ orange pods	Clays, silt, sand & gravel; sands and gravels are subrounded- subangular	Minimal to extensive; oxygenated	Pond or overbank
CSG+A	Anoxic clay through gravel	Light- dark brown & grey/ blue/green pods	Clays, silt, sand & gravel; sands and gravels are subrounded- subangular	Minimal; anoxic	Pond or overbank
SS	Silt and fine sand	Light-medium brown	Silts & fine sands	Minimal to none	Overbank or channel
FSG	Fluvial sands & gravel	Light-medium brown	Well sorted, subrounded sands and fine gravels	Minimal to none	Fluvial channel
FG	Fluvial gravels	Tan- light brown	Well sorted, subrounded fine to medium gravels	Minimal to none	Fluvial channel
FGC	Fluvial gravels & cobbles	Tan- grey	Well sorted, subrounded medium gravels to small cobbles	Minimal to none	Fluvial channel

Table II. Sediment descriptions and textures of modern sediment depositional environments used to interpret sediment in cores and cutbanks.

Modern sediment deposition analogs				
Location	Depositional setting	Observation type	Median grain size (mm)	Description
Beaver Meadows	Channel	Point count (100 particles)	3	Semi-angular to semi-rounded sand and gravel: 49% sand, 51% gravel; max grain size: 1120 mm
Beaver Meadows	Channel thalweg	Grab sample	6	Semi-angular to semi-rounded sand and gravel: 11% sand, 89% gravel
Beaver Meadows	Hillslope	Grab sample	0.5	Angular sand and gravel: <2% clay and silt; 68% sand; 30% gravel (up to 8% coarse gravel)
Moraine Park	Channel	Six point counts (100 particles)	32	Sub-rounded to rounded gravel and trace sand; medians range from 27 to 49 mm; most ranges are from 2085 mm and up to 900 mm
Moraine Park	Abandoned beaver pond	Grab sample	0.125	Dark brown to black, cohesive, fine sediment; median grain size of find sand; ~5% clay nd silt; 95% sand; <1% gravel
Corral Creek	Active beaver pond	Three grab samples	0.09	Dark brown to black, cohesive, fine sediment; median grain size of very fine to fine sand; ~3-9% clay and silt; 91-98% sand; <1% gravel

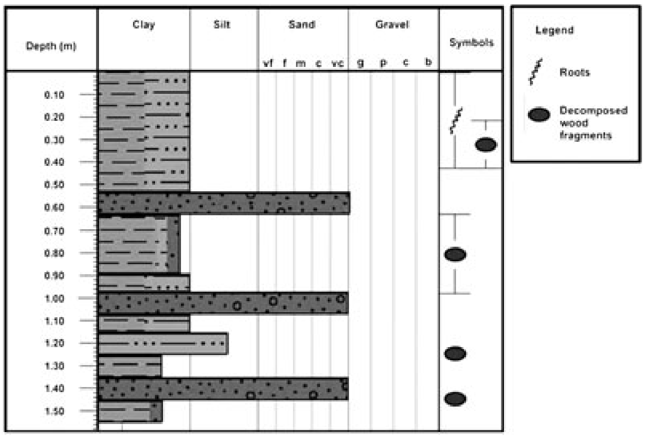

Figure 2. Sediment stratigraphy of core in northern valley of BM, representative of cores in areas of abandoned beaver ponds. Horizontal lines represent clay; horizontal lines with dots represent silt; randomly spaced dots represent sand; randomly spaced dots with circles represent gravel. The lateral extent (width of bar) of stratigraphic layers represents median grain size in that layer.

Figure 3(a)). In cores closer to the valley edge and at the upstream end of the valley, little to no silt and clay were present, contemporary soils were better developed, and mostly fine to coarse sand and fine gravel occurred in the remainder of the core. Cores and cutbanks throughout the valley in Moraine Park showed alternating sequences of fine, cohesive sediment with mostly silt and clay and minor sand, and clearly fluvial sediment ranging from well-sorted sand to gravels and cobbles (Figure 3(b)). The percentage organic material in the fine grained sediment, interpreted as beaver pond sediment, ranged from 4.9–23.2% with an average of 14.5%.

Fluvial sediment in Beaver Meadows was abundant and commonly formed most of a core or cutbank, showing upward or downward coarsening that records channel migration. When ponded sediment was present, thickness ranged from 0.05–1.2 m (Table III). Core sections with distinctly different textures were measured separately even if they were collectively interpreted as fluvial sediment. These sections ranged from a few centimeters, when bounded by clay layers as a sand lens, to over 0.5 m. Fluvial sediment packages in Moraine Park that we could core through had smaller thicknesses (Table III).

All of the cores in Moraine Park ended at a coarse fluvial sediment layer of unknown thickness, comprised of coarse gravels and cobbles, at an average depth of $0.66\,\text{m} \pm 0.36$. Ranges of the percentage of total alluvium for sediment from four different depositional settings (beaver ponds, a fluvial channel, floodplain, and abandoned channel) in Beaver Meadows and Moraine Park are reported in Table IV. In Beaver Meadows, sediment from beaver ponds comprised more of the total sediment than from fluvial channels (~42% versus 34%). In Moraine Park, there was slightly less beaver pond than fluvial sediment (37% versus 46%).

Organic material dating

Radiocarbon ages ranged from 180 to 4340 cal. years BP, with a median of 360 cal. years BP (Table V). Assuming constant aggradation over depth, aggradation rates vary over an order of magnitude from ~0.02 to ~0.47 cm yr^{-1}, with a median of ~0.22 cm yr^{-1}. Because of the large uncertainty in ages <200 cal. years BP, short-term aggradation rates should be taken as approximate rates. Aggradation rates tend to decrease with larger time interval and follow a log-linear relationship (Sadler, 1981; McShea and Raup, 1986), and we can plot these variables for relatively short timespans, over only two orders of magnitude, using a power relationship (Figure 4(a)). A large amount of variability in residuals of the aggradation rate, especially for ages <500 years BP (Figure 4(b)), indicates large temporal variability in sedimentation rates even at small timescales, which may reflect spatial variability in processes across the valley at any given time. Long-term aggradation rates are in agreement at ~0.05 cm yr^{-1}, which can be used to estimate sedimentation depths over long time periods.

A surface feature interpreted as an abandoned, partially buried beaver dam revealed, through a series of cores along a longitudinal transect, a sequence of interlayered fluvial sands and gravels and fine-grained ponded sediment (Figure 5). Several disintegrated wood fragments were found in each core, usually at the top of a fluvial coarse-grained layer. Because the buried beaver dam is still expressed as a surface feature, this must be a relatively recently abandoned dam. This is confirmed through the dating of four wood fragments (BM11, BM13, BM14, and BM15), which have ages ≤ 200 cal. years BP. We interpret this sequence as

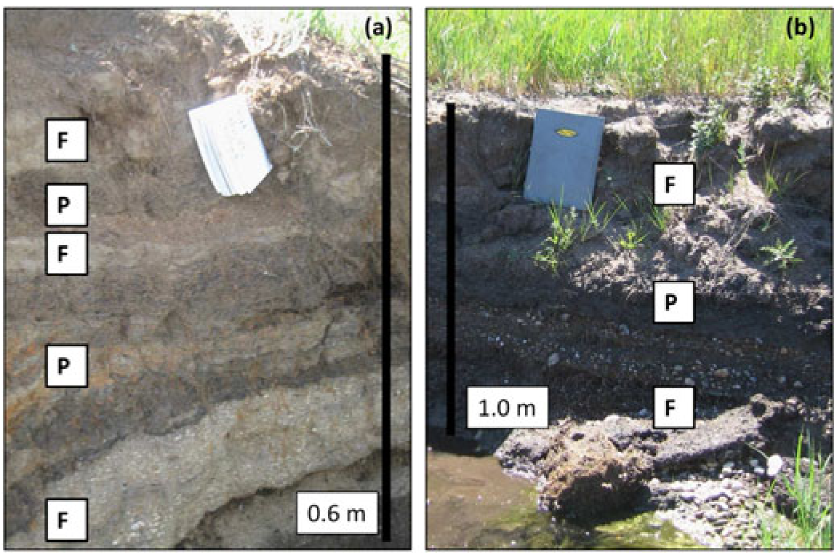

Figure 3. Photographs of cutbanks in Beaver Meadows (a) and Moraine Park (b) showing typical sequence of fluvial (F) and ponded (P) sediment. In photograph (a) a 13 x 18 cm notebook is shown for scale, and in photograph (b) a clipboard is shown for scale. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Table III. Thickness of different sediment types in cores and cutbanks, showing range of thicknesses, mean thickness, and standard deviation (SD).

	Pond sediment			Fluvial sediment		
	Range (m)	Mean (m)	SD (m)	Range (m)	Mean (m)	SD (m)
Beaver Meadows	0.05-1.20	0.25	0.17	0.05-0.60	0.21	0.12
Moraine Park	0.05-1.10	0.25	0.21	0.05-0.45	0.17	0.11

showing intermittent fluvial and beaver dam influence, either downstream or at the main break in slope (at ~5 m down valley in Figure 5) for at least 200 years and more likely up to 500 years, given that there were at least two sequences of ponded and fluvial sediment, and that the top pond-sequence dates to ~200 cal. years BP. Fluvial sediment was deposited either when an original dam was breached or simply through spatial heterogeneity of the main flow through the beaver pond. Because a beaver dam allows some flow by creating a patchy, discontinuous environment (Burchsted *et al.*, 2010), coarser-grained fluvial sediment may deposit within the pond, depending on the flow dynamics upstream of the pond.

Table IV. Percentage of examined alluvium from various depositional environments in Beaver Meadows and Moraine Park.

	Beaver pond	Fluvial channel	Floodplain	Abandoned channel
Beaver Meadows	33-50%	28-40%	2-23%	0-3%
Moraine Park	32-41%	40-52%	0-6%	0%

Beaver dams and channel complexity

Aerial photographs in Moraine Park and Beaver Meadows show significant changes in channel planform, ponding, and vegetation type and extent from the late 1930s to the present (2010). Currently there are no tall willows and very few short willows and only scattered birch and alder in Beaver Meadows. In 1938 large patches (up to 300 × 50 m) of shrubs, which are most likely willows, are present, and somewhat more fragmented patches are seen in 1947. Through the 1960s these willow patches became more linear, found in discontinuous areas along the channel. The 1987 and 2001 aerial photographs show similar conditions to those during field visits in 2009; woody vegetation is sparse and only found along the channel.

From the 2001 aerial photograph, lighter-colored vegetation areas correspond to hummocky, wet areas in the field with the top layer of sediment commonly composed of cohesive clay and silt with grasses and sedges growing on top of the hummocks. Typically a linear feature bounds these vegetation areas along the down-valley boundary, and the area tapers in the up-valley side; in that case, we interpreted these as former beaver ponds. The berms or down-valley boundaries, interpreted as locations of beaver dams, could be more clearly delineated than the entire pond boundary and were identified on a series of five aerial photographs (1938–1987). On the most recent aerial photograph (2001), we mapped linear features for which there was geomorphic field evidence of buried dams (Figure 6). We see a general decreasing trend in the presence of features representing buried beaver dams, which corresponds with beaver surveys of Beaver Meadows that show a population of 36 in 1940 and none present in 1980. Relict beaver dams identified in the aerial photographs numbered 6 in the main valley (MV) and 4 in the north valley (NV) in 1938, which only had partial photographic coverage; these numbers become 8 and 4, respectively, in 1947, 5 and 3 in 1964, and 1 and 3 in 1969 and 1987. The total topographic features identified in the field in 2009 that were interpreted as buried beaver dams were 10 in the main valley and 7 in the north valley.

A qualitative review of the aerial photograph series from Moraine Park clearly shows a dramatic decrease in the complexity of the channel network (Figure 7). Currently, the channel splits at the upstream end of the valley into two main channels and rejoins at the downstream end of the valley; there are a few other side channels on each main fork. Aerial photographs from the 1940s and 1960s show an extremely complex network of channels, where braidplains, meander belt widths, and significant riparian vegetation occupy ~50% of the valley area. In the 1987 and 2001 photographs, these areas make up <25% of the valley area.

The number of ponds and the total channel length generally decrease with time through the twentieth century, but both metrics increase in 1969, which could reflect a mild drought at the beginning of the 1960s and higher than normal discharge at the end of the 1960s (Woodhouse, 2001). Even with a decreasing beaver population in the 1960s, the newly abandoned channels would accommodate the increase in flow and appear as an increase in the number of active channels in the aerial photograph. The discharges at the time of the photographs are unknown but they were all taken during the same time of year in the early autumn. The number of ponds range from 64 in 1947, up to 96 in 1969, decreasing to only 4 in 2001 (Figure 8). The total channel length ranges from approximately 30 km in the 1940s and 1960s and drops off to less than 15 km in 1987 and 2001. Several channels that were active in the 2001 photograph were found to be abandoned during field work in 2009–2010. The braiding index for the channels, as measured from the number of channels per valley width in 18 valley-wide transects, also increases slightly for the 1960s, but the maximum is in 1964 rather than 1969. According to an ANOVA comparison of braiding indices, there are two significantly different groups of means, 1947–1969 and 1987–2001, where the means are 0.0110 (1947), 0.0125 (1964), and 0.0123 (1969), versus 0.0051 (1987) and 0.0038 (2001).

Field reconnaissance of evidence of beaver dams or beaver-chewed wood indicates that in over half of the observations of abandoned beaver dams, there is an island that has formed directly downstream (Figure 9, Figure 10). If there was no island downstream, the channel split (~25% of observations) or there was a sharp bend in the channel. After the dam is abandoned, the channel migrates and incorporates the relict dam into the streambank, where the bank is highly reinforced and acts in an analogous manner to a geotechnical bank reinforcement (Figure 9). Where only beaver-chewed wood was present, this may be a disintegrated dam or simply transported beaver-chewed wood. Where abandoned beaver dams or beaver-chewed wood is present, we see strong field evidence of the presence of channel splits or islands, which increase channel complexity and increase the braiding index (Figure 8(b)).

Table V. Radiocarbon results of wood and charcoal samples from Beaver Meadows (16 samples) and Moraine Park (3 samples). The lab numbers were given by University of Arizona Radiocarbon Lab (A) or Beta Analytic Inc. (B). The IntCal09 curve was used in OxCal 4.1 to obtain calibrated ages.

ID	Lab number	Location	Observation	Depth (m)	Material	Conventional date (years BP)	Calibrated 2σ age ranges (years BP) and % probability	Weighted average (Cal. years BP)	Aggradation rate ($cm\,yr^{-1}$)	Sediment description
BMO1	B288589	BM	Core	1.30	Wood	310 +/− 40	**350-550 (95.4)**	450	0.289	Clay, silt, fine sand; dark brown- black
BMO2	A15351	BM	Core	1.41	Wood	505 +/− 90	379- 452 (9.3), **486–725 (86.1)**	590	0.238	Clay, silt, fine sand; dark brown- black; organic
BMO3	B288590	BM	Core	0.99	Charcoal	170 +/− 40	56-97 (17.5), 124–178 (12.9), **184–291 (46.5)**, 303–355 (18.4)	210	0.471	High clay content mixed with fine to medium sand; grey- black
BMO4	B288591	BM	Core	0.99	Wood	140 +/− 40	61-105 (16.1), 116–213 (36.3), **227–343 (43)**	210	0.471	High clay content mixed with fine to medium sand; grey- black
BMO5	B288592	BM	Cutbank	0.67	Charcoal	920 +/− 40	**802-984 (95.4)**	890	0.075	Clay and silt mixed with minor fine to coarse sand
BMO7	B288593	BM	Cutbank	0.66	Charcoal	2040 +/− 40	1958-1973 (3.1), **1980–2178 (92.3)**	2080	0.032	Clay lense within sand and gravel layer; black
BMO8	A15353	BM	Cutbank	0.28	Charcoal	<130	**60-380 (93)**, 443–445 (0.1), 451–486 (2.3)	230	0.122	Clay, silt, fine sand layer between sand and gravel layers; grey-black
BMO9	B288594	BM-N	Core	0.43	Wood	110 +/− 40	**50-210 (62.5)**, 233–238 (0.8), 245–332 (32.1)	180	0.239	Clay and silt; dark brown- black
BM10	A15355	BM-N	Core	1.15	Wood	1925 +/− 70	**1764-2103 (95.4)**	1930	0.060	Clay and silt layer between coarse sand to gravel layers
BM11	B288595	BM	Core	0.76	Wood	110 +/− 40	**50-210 (62.5)**, 233–238 (0.8), 245–332 (32.1)	180	0.419	Silt and fine sand; within a layer coarsening downwards; grey-black
BM12	B288596	BM-N	Core	1.37	Wood	3140 +/− 40	3325-3369 (11.6), **3378–3509 (83.8)**	3430	0.056	Clay and silt; dark grey to black
BM13	B288597	BM	Core	0.84	Wood	110 +/− 40	**50-210 (62.5)**, 233–238 (0.8), 245–332 (32.1)	180	0.467	Clay and silt with minor sand; dark brown to black
BM14	B288598	BM	Core	0.95	Wood	130 +/− 40	66-107 (15.5), **114–212 (40.2)**, 230–340 (39.7)	200	0.473	Silt and sand coarsening downwards to fine gravel
BM15	B288599	BM	Core	0.22	Wood	110 +/− 40	**50-210 (62.5)**, 233–238 (0.8), 245–332 (32.1)	180	0.122	Clay and silt with minor sand
BM16	B288600	BM	Core	0.60	Wood	1280 +/− 40	1148- 1169 (2.8), **1185–1353 (92.6)**	1270	0.047	Clay, silt, sand, and minor gravel; transition between clay/silt and fluvial sand and gravel
BM17	B288601	BM	Core	0.60	Wood	70 +/− 40	**77- 205 (69.3)**, 274–328 (26.1)	180	0.333	Clay and silt; dark brown- black
MPO1	A15355	MP	Core	0.97	Wood	855 +/− 100	632-638 (0.3), **712–1023 (95.1)**	870	0.111	Silt and clay with minor amount of fine sand; dark brown to black
MPO2	A15356	MP	Cutbank	0.38	Charcoal	265+/−85	56- 103 (6.8), 130–177 (4.1), 191–290 (19.2), **304–563 (65.4)**	360	0.106	Silt and sand layer directly above contact with rounded cobbles; medium brown
MPO3	A15357	MP	Cutbank	1.00	Wood	3850 +/−55	4155-4186 (3.6), **4205–4480 (91.8)**	4340	0.023	Silt and clay layer; dark brown

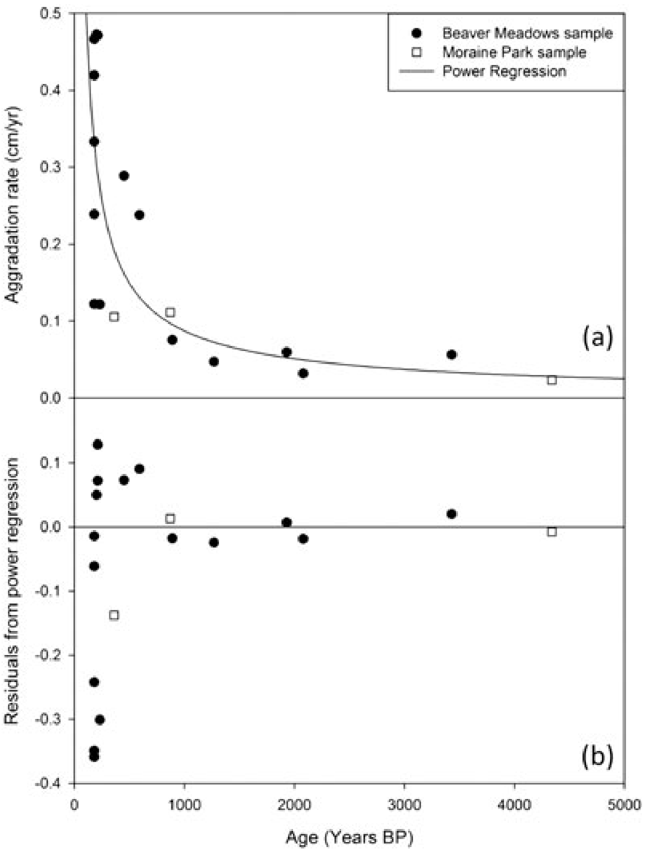

Figure 4. (a) Plot of ages versus calculated aggradation rates of sampled wood and charcoal (Table V) in BM and MP, and the power regression line fit to the data. (b) The residuals of the sampled dates from the power regression show general agreement in long-term aggradation rates and high variability in short-term rates.

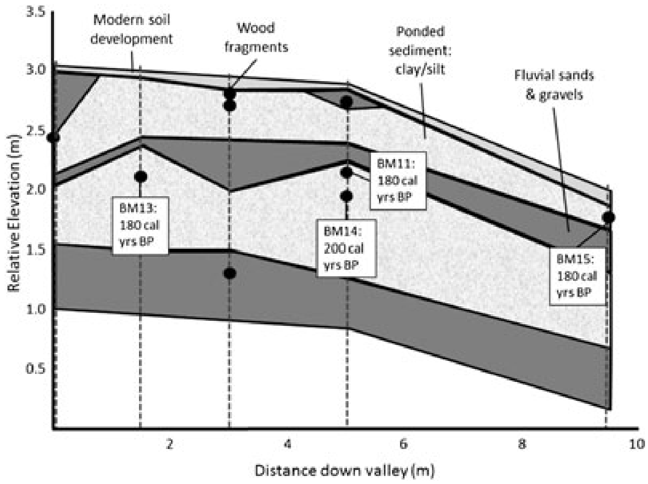

Figure 5. Schematic down-valley cross-section of topographic berm in main valley of BM, interpreted as buried beaver dam. Schematic compiled from five cores (shown as dashed vertical lines) taken along the same longitudinal transect. Four wood samples from these cores were taken and radiocarbon dated. The step in the longitudinal profile at ~5 m down valley is interpreted to be a buried beaver dam.

Discussion

Sedimentation types

Near-surface alluvial sediment in Beaver Meadows and Moraine Park creates a relatively thin veneer above glacial outwash or till (Kramer *et al.*, In press). The post-glacial alluvium displays spatial heterogeneity of sediment types laterally and within a vertical section. The various sediment types reflect deposition in fluvial channels, beaver ponds, and floodplains. Common sediment packages have alternating coarse fluvial sediment (sands and fine gravel in Beaver Meadows and gravels and small cobbles in Moraine Park) and fine-grained ponded sediment (clay, silt, and fine sands). Sediment from beaver ponds consists of mainly 0.1-m-thick sequences, up to ~1 m thick in some places, but together these sequences compose a significant proportion of the entire sampled sediment. Beaver pond sediment constitutes 33–50% of post-glacial alluvium in Beaver Meadows, and in-channel sediment constitutes only 28–40% of the alluvium. These values are supported by the geophysical analyses of Beaver Meadows, where 32–38% of alluvium was interpreted as beaver pond sediment (Kramer *et al.*, In press). In Moraine Park there is 40–50% fluvial sediment and slightly less ponded sediment (32–41%). We interpreted minor amounts of sediment (2–23% in Beaver Meadows, 0–6% in Moraine Park) as overbank deposition. We observed no other major sources of sediment, including debris flows or peat accumulation. Therefore, we interpret the primary processes for retaining post-glacial alluvium and building floodplains in Beaver Meadows and Moraine Park as reflecting the long-term dynamic interplay between channel processes and beaver pond development.

Rates of sedimentation

Sedimentation rates in Beaver Meadows and Moraine Park vary over an order of magnitude. Long-term rates agree at ~0.05 cm yr^{-1}. Short-term rates vary considerably, indicating high temporal variability in aggradation and spatial variability in sedimentation processes and rates throughout the valley at any given point in time. Recent rates of sedimentation (within 500 cal. years BP) range from ~0.1–0.5 cm yr^{-1}, which is still considerably lower than those measured in contemporary beaver ponds. Butler and Malanson (1995) measured rates of 2–28 cm yr^{-1} (mean: 9.6, sd: 8.14) in several successive beaver ponds in Montana. Other studies have obtained rates within a similar order of magnitude. John and Klein (2004) measured a mean rate of 8.02 cm yr^{-1} (sd: 3.71) and Meentemeyer and Butler (1999) measured a mean rate of 15.25 cm yr^{-1} (sd: 12.6) in beaver ponds in Germany and Montana, respectively. Aggradation rates in an entrenched channel after the introduction of beaver in eastern Oregon were at first very high (47 cm yr^{-1}) and leveled off to 7.5 cm yr^{-1} after six years (Pollock *et al.*, 2007). Ives (1942), who worked in northern Colorado, suggested a rate of $<$1 cm yr^{-1}. This is consistent with the highest rates measured in Beaver Meadows and Moraine Park, but is an estimate from observations of rising water levels over 20 years. Assuming that seasonal aggradation rates in beaver ponds in Beaver Meadows and Moraine Park are similar to those reported elsewhere, the lower averaged rates observed in Beaver Meadows and Moraine Park confirm temporal variability in sedimentation. If beaver pond sedimentation occurred within a similar order of magnitude as that measured in contemporary ponds, averaged sedimentation rates observed in Beaver Meadows and Moraine Park represent periods of relatively fast pond sedimentation and periods of slow or episodic fluvial sedimentation.

Because these low-gradient, broad valleys on the eastern side of the Continental Divide in RMNP are not affected by many outside sediment sources (e.g. debris flows, frequent fire- induced sedimentation), they are an ideal location for examining the potential of beaver-induced sedimentation in this geographic setting. Compared with sites on the western slope of the divide in RMNP that are subject to extensive debris-flow deposition (Rubin, 2010), Beaver Meadows and Moraine Park have limited sources of hillslope sediment. Aggradation rates at the western site are nonetheless consistent with those in Beaver Meadows

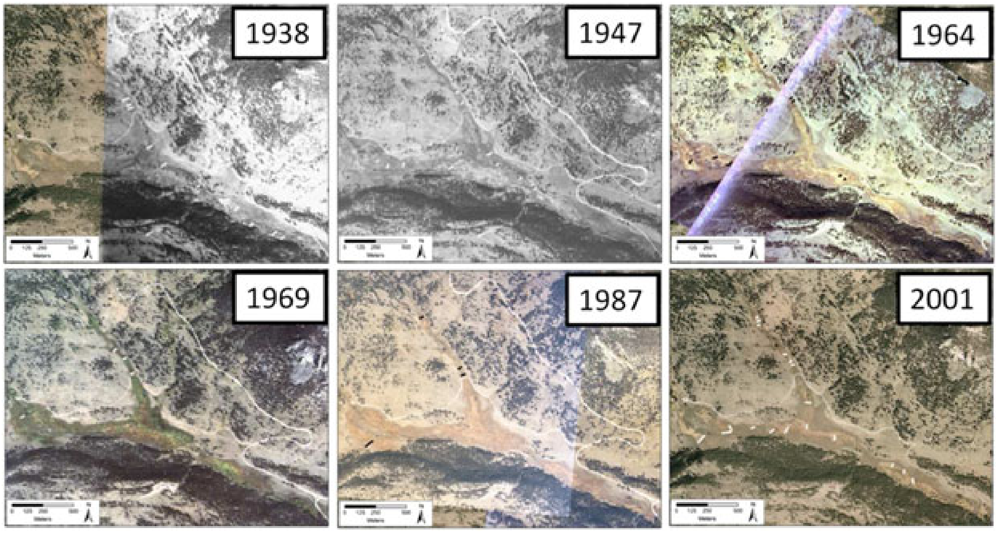

Figure 6. Aerial photograph series of Beaver Meadows from 1938–2001. Photos from 1938–1987 show black or white lines (depending on photograph darkness) that represent interpreted active or abandoned beaver dams. White lines on the 2001 photograph are located where there was photographic or field evidence (in 2009–2010) of buried beaver dams. Where there is incomplete coverage of the valley (1938 and 1964), the 2001 aerial photograph is in the background. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

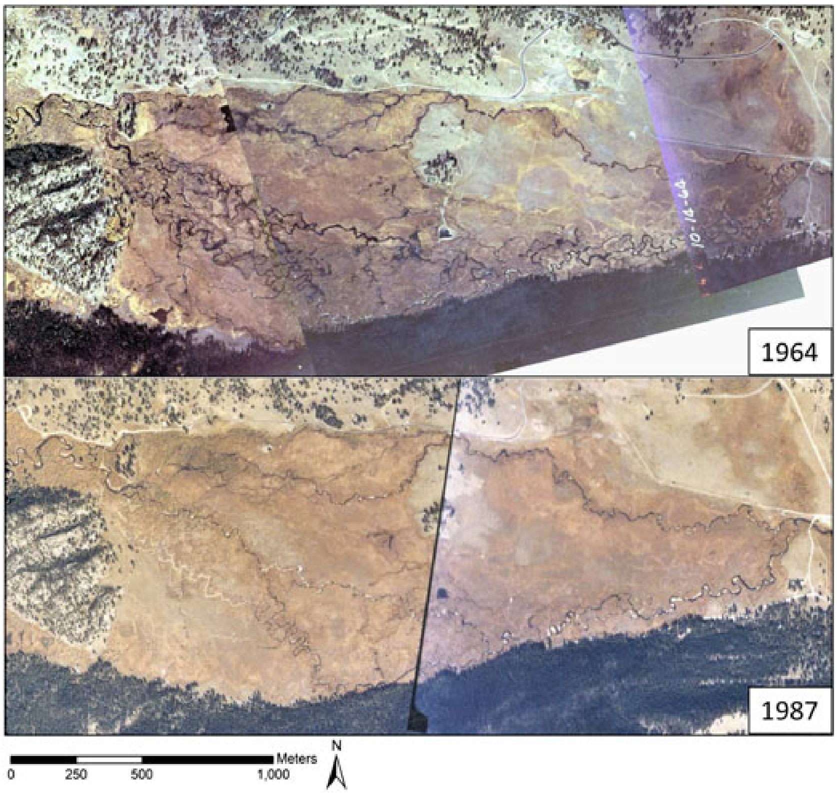

Figure 7. Aerial photographs of Moraine Park in 1964 and 1987 that show the dramatic decrease in channel complexity and total channel length. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

and Moraine Park, ranging from 0.04–0.15 cm yr^{-1}, with more recent rates up to 0.4 cm yr^{-1} (Rubin, 2010). In a site more similar to Moraine Park, Horseshoe Park on the eastern slope of RMNP shows varying Holocene sedimentation rates of 0.025 cm yr^{-1} directly after deglaciation to 8200 years BP, 0.089 cm yr^{-1} from 8200–6075 years BP, and 0.035 cm yr^{-1} from 6075 years BP to present (Rainey, 1987). The average of these values (0.05 cm yr^{-1}) coincides with the long-term average aggradation rates in Beaver Meadows and Moraine Park. The long-term rates of aggradation, which agree in sediment sinks throughout RMNP, may reflect the overall landscape change and the average amount of sediment available from the hillslopes and headwaters per year. However, in each depositional setting, the unique amalgam of sediment types, rates, and incision or transport processes reflects the nearby hillslope and floodplain processes throughout the Holocene.

Beaver, channel complexity, and sedimentation positive feedback loop

The presence of beaver dams increases the complexity of the channel network through promoting avulsions, multiple flow paths, and discontinuous flows (Woo and Waddington, 1990; John and Klein, 2004; Burchsted *et al*., 2010). The dramatic decrease in the braiding index and total channel length from the 1930s to the present in Moraine Park was concurrent with a

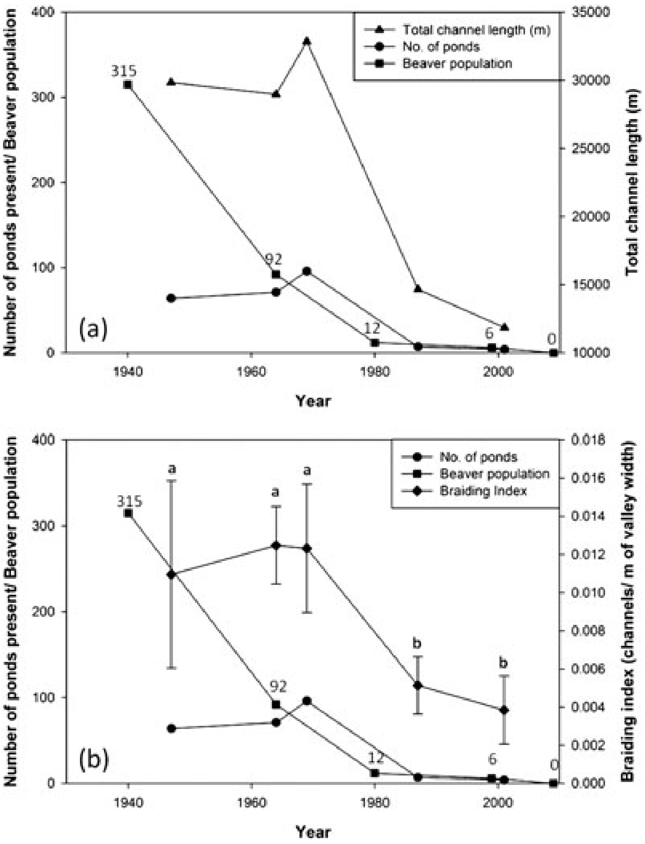

Figure 8. Relationship between channel complexity and number of beaver ponds (circles) in Moraine Park. Actual beaver populations are shown on graph, as determined from surveys conducted by RMNP (squares). Channel complexity is represented by total channel length (a) and braiding indices (b). Letters above braiding indices in graph (b) signify significantly different groups. Note that there is a general correspondence in trend of changes in channel complexity (total channel length and braiding indices) and number of ponds.

surveyed decrease in beaver population and a decrease in the number of ponds present. These data, in conjunction with field evidence of islands or channel splits downstream of relict beaver dams, support the hypothesis that beaver promote the formation of a multi-thread channel network. Past studies have noticed similar changes over shorter time spans (Woo and Waddington, 1990; John and Klein, 2004). The multi-thread network influences complexity in several spheres, such as the vegetated riparian area, groundwater flow, and sedimentation (Westbrook *et al.*, 2006; Burchsted *et al.*, 2010; Westbrook *et al.*, 2011). Moraine Park illustrates the extended result of the removal of beaver on channel planform and reduction of multiple flow paths during overbank flooding, and the resultant transformation of riparian vegetation zones to xeric environments. The reduction of beavers removes current floodplain processes from the range of historical variability of valley bottom processes in terms of channel complexity, sedimentation, and how these geomorphic factors influence ecologic process and form.

In terms of hypothesized beaver pond sedimentation in a beaver-meadow complex, the increase in channel complexity forms a positive feedback. A multi-thread channel network, a product of beaver dams, increases the potential channel length for further damming, thus increasing the area that can be occupied by beaver ponds and increasing the volume of beaver pond sediment trapped in a valley (Figure 11). With relatively few beaver dams, complexity is reduced and the potential of beaver ponds to trap sediment is minimal. There is probably a threshold population of beavers that will alter channel planform and exponentially increase possible dam sites and thus beaver population. Even though sedimentation is spatially heterogeneous because of the different processes acting on a broad valley at any point in time, beaver ponds can exist at multiple locations laterally and longitudinally throughout an extensive valley like Moraine Park.

The beaver-meadow complex hypothesis was introduced as a mechanism to explain the presence of fairly large magnitudes of fine sediment in glacially-carved valleys as opposed to the previous explanations of silted-up glacial lakes, meandering streams, and braided channels (Ruedemann and Schoonmaker, 1938; Ives, 1942; Rutten, 1967). Until now, this had not been tested quantitatively by determining the percentage of the entire alluvium influenced by beaver dams in low-gradient valleys where sediment storage is likely. Although the hypothesis may not be applicable in all settings, we believe that Beaver Meadows and Moraine Park represent settings where beavers do have a large impact in post-glacial sediment aggradation. Given the high percentage of beaver sediment (~50%) in the thin veneer (~1–6 m) of alluvial sediment and the role of beavers in enhancing their habitat potential not only through creation of ponds but also a multi-thread

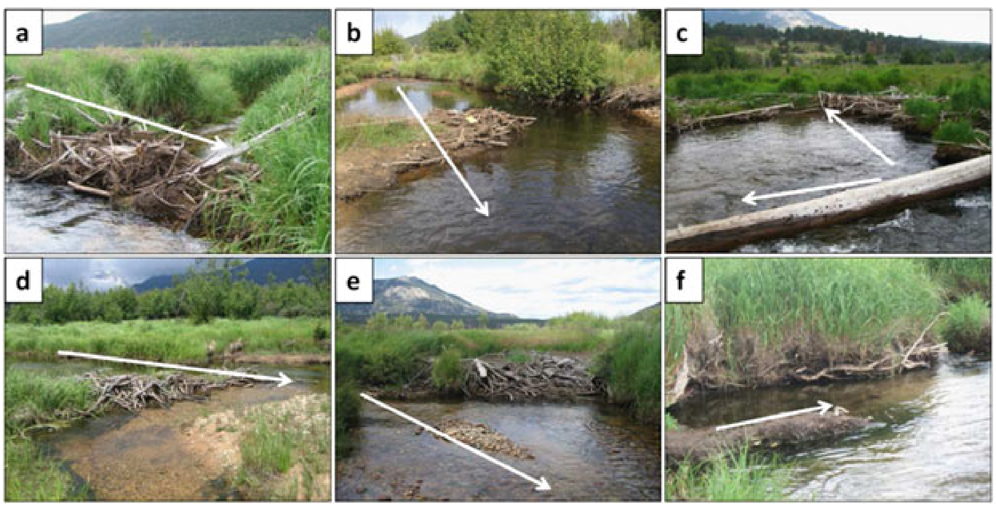

Figure 9. Examples of beaver-influencd channel form. Photos a, c, and e show channel avulsions or splits where an abandoned beaver dam is present. Photos b and d show island formation at the site of an abandoned beaver dam. Photo f shows a bank reinforced by beaver-chewed wood, possibly an abandoned dam, which caused a sharp meander bend. White arrows indicate main flow direction. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

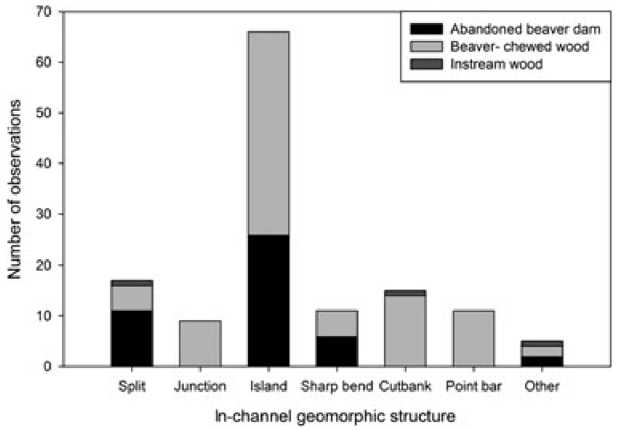

Figure 10. Geomorphic channel form associated with different types of wood in channel throughout Moraine Park. For each type of wood observation made (abandoned beaver dam, beaver-chewed wood, or instream wood (wood without any evidence of beaver influence), the main proximal channel form was characterized. Splits and junctions are where a side channel splits or rejoins; an island is smaller in width than the combination of the two side channels; a sharp bend is a meander curve with an angle of 90° or less.

channel network, valley-bottom aggradation and deposition of future streambank material has been facilitated by beavers.

Historical range of variability of beaver pond deposits

Given the scenarios of future climate change, the relevance of historical range of variability to management may be limited, because the governing processes are moving into non-stationary trends from what human society has been used to in the past centuries (Milly *et al.*, 2008). Novel scenarios, in terms of what has been seen in the historical past, may need to be considered for environmental restoration, rather than restoring to historical condition. However, given the interaction of multiple geomorphic and biotic processes in producing the current valley form, understanding the historical range of variability illuminates the template on which current conditions formed. Understanding the historical range of variability of valley bottom processes can provide insight to the possible trajectories with altered hydrologic, sediment, or disturbance regimes. Reference conditions for restoration often use a historical condition as a goal, and although this may be misleading, understanding process in conjunction with a range of historical valley bottom conditions can be thought of as a compromise between scientists who advocate a completely process-based understanding and managers who sometimes choose overly-simplistic restoration techniques. The role of biotic processes, especially animals, in shaping long-term channel form and valley evolution has largely been ignored in the past. This study has illustrated how beavers can compound their own effects on the valley through creating a more complex channel network and thus allowing more potential stream length to be dammed where sediment can be trapped. Without the added complexity of a beaver- influenced channel network, less fine sediment will be trapped and more sediment will be evacuated from the system because of the higher stream gradient (Gurnell, 1998).

In this type of headwater stream there are few segments where fine sediment will deposit. At the watershed scale, headwaters are erosional centers (Schumm, 1977), but the broad, low-gradient valleys of glacial troughs act as temporary storage depots

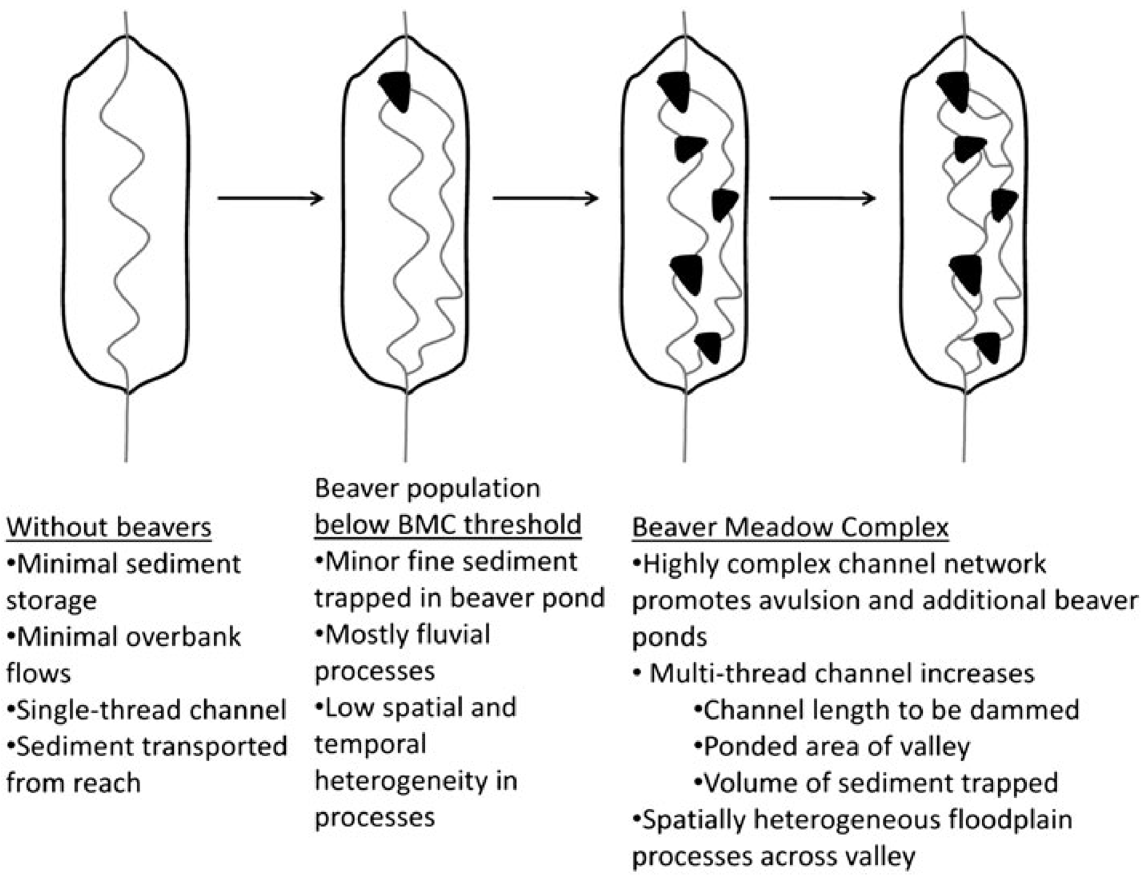

Figure 11. Schematic diagram showing change in valley planform and channel complexity with an increase in beaver population forming a beaver-meadow complex (BMC), and varying characteristics of sediment storage, channel complexity, and heterogeneity for a headwater, snowmelt-dominated system. Black rounded triangles represent beaver dams and upstream ponds. Flow direction is from top to bottom.

for sediment. Without mechanisms such as those present in beaver meadows that slow the movement of sediment, hillslope and upstream disturbances translate downstream more quickly and with greater magnitude. Just as beaver dams dampen the effect of floods (Gurnell, 1998; Westbrook *et al.*, 2006), the beaver-meadow complex in broad, low-gradient headwater valleys may dampen sediment movement. As channels migrate laterally, the fine sediment trapped in beaver ponds will form cohesive streambanks, which are rare in headwater streams because of high gradients and coarse substrates. This furthers the legacy of beavers on channel form by increasing the frequency of cohesive streambanks and thus increasing overall bank stability.

Given that estimates of beaver populations in North America prior to European settlement range from 60 to 400 million and current populations are only 6 to 12 million (Naiman *et al.*, 1988), beaver-meadow complexes would have been much more common. Butler and Malanson (2005) estimated that the number of ponds ranged from 15 to 250 million versus only 1.5 to 7.7 million before and after European settlement, respectively. Because beaver-meadow complexes are composed of several ponds, the number of complexes will be less but would still have decreased by at least 50%. Beaver-meadow complexes contribute significantly to the development of the floodplain in unconfined, low-gradient valleys, which are often disproportionately impacted by human development, thereby further altering floodplain processes from a historical range of variability throughout North America.

Conclusions

Unconfined, low-gradient headwater valleys are important centers for temporary sediment storage within the larger space and timescales of sediment transport from headwaters to the mouth of a catchment. In Beaver Meadows and Moraine Park in RMNP, we have shown the importance of beavers in trapping and storing a significant amount of fine sediment throughout the Holocene. Because the alluvium that covers the glacial sediment is relatively thin, a relatively small magnitude of sediment deposition induced by beavers is significant and supports the beaver-meadow complex hypothesis in explaining the evolution of relatively flat, broad headwater valleys with abundant fine sediment. Temporal heterogeneity in aggradation rates reflects spatial heterogeneity in fluvial and beaver pond processes throughout the floodplain. These study valleys were ideal locations for examining the potential role of beavers in floodplain processes, but relatively low sedimentation volumes in beaver ponds may be overshadowed in landscapes with strong signals from debris flows (Rubin, 2010) or sediment pulses from geomorphically-effective forest fires (Meyer *et al.*, 1995; Persico and Meyer, 2009).

Beaver were abundant in the RMNP area prior to European settlement, which caused a positive feedback in the volume of sediment aggradation through the formation of a complex channel network. The current ecologic and geomorphic condition without beaver exhibits a single-thread channel with a higher gradient, which not only traps less sediment but, with a higher stream power, incises and transports additional sediment. This condition falls outside of the historical range of variability in channel form and sedimentation rates. Historically, a multi-thread channel network maintained by successive beaver dams trapped a nearly equal amount of beaver pond and in-channel sediment. Fine sediment, which ordinarily would be flushed out of headwater reaches, is trapped and incorporated into the floodplain and streambanks after channel migration. The faster and larger magnitude of sediment evacuation translates into higher connectivity between disturbances in the headwaters and downstream reaches.

The ecological management of these headwater valleys requires an understanding of the historical channel conditions in addition to changes in vegetation and elk–beaver interactions and the impacts of past and present climate conditions. With the reduction in beaver population, the change in channel form to a simpler, single-thread system has affected riparian vegetation, sediment trapping and the potential for supporting a larger beaver population.

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