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BEAVER ASSISTED RIVER VALLEY FORMATION

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ABSTRACT

We examined how beaver dams affect key ecosystem processes, including pattern and process of sediment deposition, the composition and spatial pattern of vegetation, and nutrient loading and processing. We provide new evidence for the formation of heterogeneous beaver meadows on riverine system floodplains and terraces where dynamic flows are capable of breaching in-channel beaver dams. Our data show a 1.7-m high beaver dam triggered overbank flooding that drowned vegetation in areas deeply flooded, deposited nutrient-rich sediment in a spatially heterogeneous pattern on the floodplain and terrace, and scoured soils in other areas. The site quickly de-watered following the dam breach by high stream flows, protecting the deposited sediment from future re-mobilization by overbank floods. Bare sediment either exposed by scouring or deposited by the beaver flood was quickly colonized by a spatially heterogeneous plant community, forming a beaver meadow. Many willow and some aspen seedlings established in the more heavily disturbed areas, suggesting the site may succeed to a willow carr plant community suitable for future beaver re-occupation. We expand existing theory beyond the beaver pond to include terraces within valleys. This more fully explains how beavers can help drive the formation of alluvial valleys and their complex vegetation patterns as was first postulated by Ruedemann and Schoonmaker in 1938.
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KEY WORDS: beaver meadow; *Castor canadensis*; ecosystem engineering; floodplain; habitat heterogeneity; river valley formation; Rocky Mountain National Park; terrace

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INTRODUCTION

Beaver (*Castor canadensis* and *C. fiber*) are key ecological agents that shape riverine landscapes by influencing the hydrogeomorphic processes that connect floodplain ecosystems to streams (Gurnell, 1998). Beaver build dams across low order streams to pond water and provide protection from predators, expand foraging areas and territories, and store food over winter months (Baker and Hill, 2003). Dam building results in the transformation of terrestrial to wetland and lotic to lentic ecosystems, which alter patterns of sediment retention (Naiman *et al.*, 1986; Butler and Malanson, 2005), rates of soil nutrient cycling (Naiman *et al.*, 1994; Johnston *et al.*, 1995), organic matter and nutrient deposition and retention (Naiman and Melillo, 1984; Devito and Dillon, 1993) and vegetation succession (Terwilliger and Pastor, 1999). Historically beaver were abundant and widely distributed in North America and Eurasia. Although their populations were significantly decreased by fur trapping, they have recovered in much of North America and are increasing in Europe. Beaver have been shown to influence up to 30–50% of the total length of 5th order and smaller streams (Naiman and Melillo, 1984) in some locations. It is therefore critical to understand the influence of beaver on hydrogeomorphic processes, particularly on headwater streams which, for example, comprise ~85% of total stream length in the USA (Leopold *et al.*, 1964).

The existing model of beaver meadow formation provides a conceptual framework for testing the hydrogeomorphic influence of beaver on riverine landscapes. Beaver alter plant communities by building dams that impound water in upstream ponds and reduce stream velocity. Ponds can also inundate adjacent riparian areas, which may drown existing vegetation. They also function as efficient water and sediment traps, and may fill with fine-grained, nutrient-rich sediment and organic materials (Bigler *et al.*, 2001). Sediment can remain in the pond area when dams are abandoned on small streams (Butler and Malanson, 2005) or if there is non-repairable channel evulsion around the dam while it is active (Cooper *et al.*, 2006). The water table recedes as dams degrade and the bare, moist, nutrient-rich sediment of abandoned ponds is quickly colonized by herbaceous plants or shrubs, forming what has been termed a beaver meadow (Ives, 1942; Johnston and Naiman, 1987). Beaver meadows are relatively homogeneous patches of distinct plant communities that increase heterogeneity at the landscape scale (Remillard *et al.*, 1987; McMaster and McMaster, 2000; Wright *et al.*, 2002). Beaver meadows may

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persist for decades as patches dominated by herbaceous or shrubby plants (Neff, 1957; Barnes and Dibble, 1988; Terwilliger and Pastor, 1999). Alternatively, the loss of beaver from riverine systems can dry floodplains, which can lead to desertification or upland forest development (Wolf *et al.*, 2007; Bilyeu *et al.*, 2008; Green and Westbrook, 2009).

Early geological research published in *Science* suggested that 'beavers are able to aggrade all smaller valleys [in the northern half of North America] below the size of navigable rivers...originally in small descending steps, which disappear in time and leave a gently graded...plain horizontal from bank to bank' (Ruedemann and Schoonmaker, 1938). Their hypothesis suggested beaver may have assisted the formation of fertile alluvial valleys that developed during the thousands of years since glaciers receded, but they provided very little empirical evidence to support this far-reaching hypothesis. Existing beaver meadow formation theory does provide a framework and some empirical evidence to support the concept that for headwater streams the pond is the main hydrologic feature produced by dams (Bigler *et al.*, 2001). But this concept does not explain how beaver may affect landscapes beyond the pond.

Beaver dams built on larger streams with dynamic flows often fail rather than become abandoned, causing stored sediment to be flushed downstream and ponds not to form beaver meadows (Butler and Malanson, 2005). Our previous research, however, showed how beaver dams across a 4th order reach of the Colorado River greatly enhanced the extent, depth and duration of flooding associated with high flows, and that these effects were observed on terrace elevations above the 100-year floodplain (Westbrook *et al.*, 2006). Thus, beaver dams built on streams may have ecological and geomorphological consequences far beyond their within-channel ponds. Here, we investigate the processes of beaver meadow formation in a riverine system where dynamic flows tend to frequently breach within-channel dams. We examine how beaver dams affect a suite of key ecosystem processes, namely (1) the pattern and process of sediment deposition, (b) the composition and spatial pattern of vegetation and (3) nutrient loading and processing. Then, we place our results within ecological context and suggest a new paradigm that moves beaver meadow formation theory beyond the pond. Under the new paradigm, dams built in headwater stream systems would lead to the formation of small, homogeneous beaver meadows in stream channels and on floodplains, whereas dams built on higher order stream systems would lead to the formation of potentially spatially expansive, heterogeneous beaver meadows on terraces. This new paradigm more fully explains the hydrogeomorphic influence of beaver on riverine landscapes.

METHODS

We worked in the riparian corridor of the Colorado River in Rocky Mountain National Park (RMNP), Colorado, USA. The river through the study reach is 4th order, has a pool-riffle form, meanders and has a snowmelt-driven hydrological regime. Mean daily discharge ranges from $14.7\,m^3\,s^{-1}$ in spring to $1.8\,m^3\,s^{-1}$ during late summer base flow. Suspended sediment concentrations at the downstream U.S. Geological Survey gauging station (#09010500) are 0.5–217 $mg\,L^{-1}$. The floodplain averages ~1 m in elevation above the channel bottom and is 0–25 m wide. The remainder of the 0.6 km wide valley is a terrace 0.7–1.2 m above the floodplain (Woods, 2001). Vegetation in the valley is a riparian shrubland dominated by *Salix monticola*, *S. geyeriana* and *S. planifolia*, and dry and wet meadows dominated by *Deschampsia cespitosa*, Calamagrostis canadensis and *Carex utriculata*. The valley is intensely browsed by elk (*Cervus elaphus* nelsoni) and moose (*Alces alces* shirasi), which appear to have reduced shrub height and vigour as in other areas of RMNP (Baker *et al.*, 2005). Plant nomenclature follows Weber and Wittmann (2001). A more detailed description of the study site can be found in Westbrook *et al.*, (2006).

Beaver built an L-shaped dam across the Colorado River in August 1997 (Woods, 2001), which remained intact until breached by high streamflow on 29 May 2003. The dam was 1.7 m high and 30 m wide, extended 35 m upstream along the west side of the river channel, and diverted 70% of the Colorado River volume onto the floodplain and terrace (Woods, 2001), flooding 8.7 ha in 2002 (Westbrook *et al.*, 2006). Diverted river water that flowed westerly across the floodplain and terrace was also dammed by beaver. During 2002, there were about 6 small beaver dams (0.1–0.5 m tall and 0.3–100 m wide) present on the floodplain and terrace that decreased water velocity and increased its depth and distribution.

We used a non-aligned, systematic sampling design to analyse sediment accumulation, sediment character and vegetation composition following beaver dam failure. UTM coordinates for the corners of a 180 m × 240 m area that was hydrologically influenced by the dam (i.e. was either flooded or had an elevated groundwater table) (Westbrook *et al.*, 2006) were obtained from a geo-referenced 2001 aerial photograph in June 2003. The study area was gridded into 10 × 10 m cells and the UTM coordinates of the centre of a 1 × 1 m plot within each cell ($n = 432$) was randomly generated using a macro in Microsoft Excel. A GPS with a horizontal accuracy of 2–4 m was used to find the centre of each plot and this point was marked by a nail wrapped in flagging tape (Figure 1a). Thirty-one plots of the 432 plots were within the active river channel or a deep-water oxbow and not used. A 1 × 1 m sampling quadrant, made of

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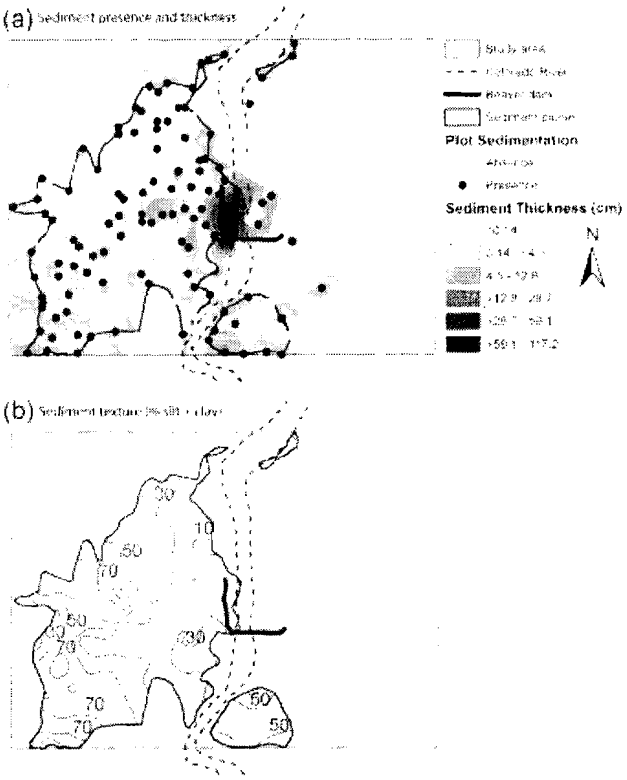

Figure 1. Map showing sediment presence and absence for plots, sediment thickness, and texture (% silt + clay) delineation of the deposits of sediment within the study area (180 m × 240 m). Sediment was deposited (at 112 out of 401 plots) primarily west of the Colorado River where sediment-rich river water flowed into the riparian area. Sediment thickness and percent sand decreased with distance from the river channel

2.54-cm diameter PVC and divided into four equal sub-quadrants, was centred on the nail at each of the remaining 401 plots.

The elevation of the plot centre was determined using a 0.30 m digital elevation model generated with photogrammetric methods (IntraSearch, Denver, Colorado). Plots were categorized as being hydrologically disturbed or undisturbed during the beaver occupation. A combination of water table elevation maps and flooding extent maps (Westbrook, 2005), field notes, aerial photographs and still photographs were used to create indices of plot disturbance. Classes for the hydrologically disturbed by beaver metric were either (0) undisturbed or (1) disturbed, i.e. was either flooded or experienced an elevated water table. A flood index for the last 3 years of beaver occupation was created with the classes; (1) deeply flooded (>0.50 m depth), (2) shallowly flooded (0.05–0.50 m depth) and (3) rarely or never flooded. Similarly, a surface soil wetness index was created after beaver occupation, with the classes (1) moist to wet, and (2) dry, determined by feeling the samples at the time of sediment sampling and also recording microsite conditions (i.e. hummock vs. hollow).

Sediment thickness was measured in two random locations within each of the four sampling sub-quadrants with a hand-held corer in August 2003 to estimate net sediment accumulation within each plot. The mean of the eight sub-samples was used as the measure of sediment thickness for each plot. Each core was visually inspected to locate the interface between the sediment deposited over the last 6 years and the buried soil. We defined deposited sediment as lacking soil development. Sediment thickness was re-sampled at 20 randomly chosen plots to test the precision of identifying the sediment-soil interface. A paired t-test showed sediment thickness did not differ between the two sample periods ($p = 0.29$).

Replicates for each plot were pooled in a polypropylene bag, dried at 60°C for 5 days, and particle size determined using the hydrometer method (Gee and Bauder, 1986). 5–10 g of soil from each plot were hand-ground into a powder and analysed for total organic carbon (TOC, as samples tested negative for inorganic carbon using HCl) and total nitrogen (TN) on a LECO CHN1000 analyser (LECO, St. Joseph, Michigan, USA). Total phosphorus (TP) was measured by first digesting samples with nitric-perchloric and analysing the digests using inductively coupled plasma. Kriging was used to model the spatial variation in sediment thickness and % fine sediment (silt + clay) and calculate the total amount of sediment deposited on the floodplain and terrace. Spatial analyses were conducted using Surfer ver. 7 (Golden Software Ltd., 1999).

The ion exchange resin bag technique (Binkley, 1984) was used to assess nutrient (N and P) availability 13 months following the beaver dam breach as it was believed to be a reasonable index time for understanding the long-term effects of the dam on soil fertility. Resin bags were prepared by sealing 14 ml of anion resins and 14 ml of cation resins in separate pouches of a nylon stocking. One bag was buried at 5 cm depth in the centre of each plot between 8 June and 23 August in 2004. Resin bags were recovered from 181 (45%) of the 401 plots; bags were not recovered from the remaining plots where plot markers were lost due to deep sediment burial. Recovered bags were desorbed in 100 ml of 2 M KCl and shaken mechanically for 1 h. The KCl extracts were filtered through Whatman #42 filters and frozen for later analysis. Thawed extracts were analysed for total inorganic N (NH_4^+–N plus NO_3^-–N) and PO_4^{3-}–P colorimetrically on an Alpkem automated flow system.

Plant species composition and per cent canopy cover by species was determined in a 1 m^2 quadrant at each of the 393 plots in August 2004. Canopy cover was visually separated into the following six cover classes (%): <1, 1–5, 6–25, 26–50, 51–75 and 76–100. The number of *Salix* spp. and *Populus tremuloides* seedlings present in each plot was recorded. A species accumulation curve (Soberón and Llorente, 1993) reached an asymptote after 140 plots,

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indicating our sampling effort fully captured the composition and richness of the beaver affected area. Multivariate statistical analyses were used to examine floristic relationships among the plots. Six plots with <1% plant cover and three plots with incomplete data sets were not included in the analysis. A primary matrix was constructed containing per cent cover (midpoint of cover classes) for 82 plant species in the 384 plots used in the final analysis. Major gradients in vegetation composition were identified using the indirect ordination technique Detrended Correspondence Analysis (DCA). Agglomerative cluster analysis with Sorensen distance was used to create the dissimilarity matrix and average linkage grouping method to construct the dendrogram that we used to develop a vegetation classification. Two plots had 100% cover of just one species (either *Picea engelmannii* or *Salix* spp.) and formed their own clusters. These plots were subsequently removed and the analysis re-run. Indicator analysis (Dufrene and Legendre, 1997) was used to identify significant ($p < 0.05$) indicator plants of each plant community (cluster). PC-ORD ver. 4.14 (McCune and Mefford, 1999) was used for vegetation analyses.

RESULTS

Sediment deposition

Sediment was deposited in 28% (112) of the 401 plots sampled, and deposition was heterogeneous on the floodplain (Figure 1a). The thickness of deposited sediment in plots that received sediment averaged 6.0 cm (SE = 1.6 cm), and ranged up to 120.0 cm. Sediment was deposited in two main plumes (Figure 1a), a 1.1 ha plume west of the Colorado River and a 0.2 ha plume east of the river. The western plume contained ~750 m^3 of sediment and occurred where the majority of Colorado River water was diverted by the dam onto the floodplain. The percentage of fine sediments (silt + clay) in it increased exponentially from 30 to 70% as distance from the river increased (Figure 1b; $r^2 = 0.27$, $p < 0.0001$). The eastern sediment plume accumulated after the beaver dam breached, which created a downstream flood into areas that were not inundated when the dam was intact. It was relatively homogeneous with ~50% silt + clay.

Vegetation composition

Eighty-one vascular and one non-vascular plant species were found in the study plots and six communities were identified using cluster analysis. Community 1 included 224 plots with high canopy coverage of the sedges *Carex utriculata* (CAUT) and *C. aquatilis* (CAAQ) and occurred in areas shallowly flooded during beaver occupation, that received little new sediment deposition, and were wetter than other communities following beaver occupation (Table I). Community 2 included 73 plots dominated by the early successional species *Agrostis scabra* (AGSC) and *Poa palustris* (POPA) and occurred in areas where bare mineral sediment was created by river scouring or deep sediment burial. These areas were deeply flooded during the beaver occupation and generally wetter than other communities following it. Community 3 included 75 plots that were not inundated by the beaver flood, and supported either the (i) dry meadow indicator species *Deschampsia cespitosa* (DECE), *Taraxacum officinale* (TAOF), and *Achillea lanulosa* (ACLA) or (ii) wet meadow indicator species *Carex canescens* (CACA). Community 4 included eight plots with tall hummocks where *Salix monticola* (SAMO), *Carex microptera* (CAMI) and *Polemonium caeruleum* (POCA) survived the multi-year period of inundation. Community 5 included three plots with the indicator species *Phleum pratensis* (PHPR) and *Critesion jubatum* (CRJU) in flood disturbed areas that were drier than other communities in the post beaver period. Community 6 included two plots with indicator species *Plantago major* (PLMA) and *Antennaria* spp. (ANSP) that occurred in an area >1 m above the flood elevation and were dry before and following beaver occupation.

A total of 95 willow seedlings from the 2003 or 2004 cohorts were found in 48 (11%) of the plots. These had established on the mineral sediment plume west of the river and in areas east of the river where deep water during the beaver dam period drowned the vegetation and exposed bare soil. Ninety per cent of the willow seedling occurrences were in plots of the *C. utriculata*/*C. aquatilis* and *A. scabra*/*P. palustris* communities (Table I). Seven aspen seedlings were found in six plots, mainly on the western sediment plume (Table I).

The two-dimensional DCA model (Figure 2) has good dispersion of the plots. These separations reflect differences in flooding and water availability before and after the beaver occupation and disturbance during the beaver occupation (Table I). The first DCA axis (eigenvalue = 0.654) separated community 1 (right) from community 3 (left). This axis represents a gradient of increasing moisture conditions (from left to right) during the period of beaver occupancy. The second axis (eigenvalue = 0.437) separated community 4 (top) from community 2 (bottom), and represents a gradient of decreasing disturbance, separating vegetation that survived the beaver occupation near the top, from vegetation that established on bare soil in the post beaver period at the bottom. The high spatial variation in environmental conditions during and following beaver occupation likely influenced the heterogeneous and complex riparian landscape present after beaver occupation (Figures 3 and 4).

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Table I. Summary of the environmental measures in the six plant communities identified using cluster analysis

Environmental measure	Plant community					
	1. CAUT/ CAAQ	2. AGSC/ POPA	3. TAOF/ ACLA	4. SAMO/ CAMI	5. PHPR/ CEJU	6. PLMA/ ANSP
Plot frequency	224	73	75	8	3	2
Richness (species/1m^2)	6.3	9.5	9.2	9.4	5.3	12.0
	(0.2)	(0.3)	(0.3)	(1.3)	(1.5)	(1.0)
Elevation above arbitrary datum (m)	0.87	1.04	1.12	0.60	1.35	1.50
	(0.04)	(0.10)	(0.07)	(0.08)	(1.09)	(0.00)
Hydrological disturbance by beaver[a]	0.8	0.9	0.6	0.5	1.0	0.5
	(0.0)	(0.0)	(0.1)	(0.2)	(0.0)	(0.5)
Sediment accumulation (cm)	0.7	2.4	1.3	0.1	0.0	0.0
	(0.1)	(0.5)	(0.4)	(0.1)	(0.0)	(0.0)
Silt + Clay (%)	38	42	43	59	NA	NA
	(1)	(3)	(3)	NA	NA	NA
TN (g N/kg soil)	1.34	1.71	1.64	4.23	NA	NA
	(0.06)	(0.12)	(0.12)	NA	NA	NA
TOC (g C/kg soil)	22.3	26.1	25.4	74.4	NA	NA
	(1.1)	(1.8)	(1.7)	NA	NA	NA
TP (kg P/kg soil)	0.87	0.96	0.94	1.42	NA	NA
	(15.9)	(29.2)	(28.9)	NA	NA	NA
Resin-N (mg N/bag)	1.42	0.34	1.08	1.89	NA	1.29
	(0.39)	(0.09)	(0.50)	(0.92)	NA	(0.03)
Resin-P (mg P/bag)	0.10	0.02	0.09	0.41	NA	0.30
	(0.01)	(0.00)	(0.02)	(0.27)	NA	(0.04)
Flood index during beaver occupation[b]	2.0	1.5	2.1	2.4	1.3	2.5
	(0.0)	(0.1)	(0.1)	(0.3)	(0.3)	(0.5)
Wetness index following beaver occupation[c]	1.7	1.6	1.7	1.8	2.0	2.0
	(0.0)	(0.1)	(0.1)	(0.2)	(0.0)	(0.0)
Willow seedling occurrence (no.)	25	19	2	0	1	1
Aspen seedling occurrence (no.)	2	4	0	0	0	0

Values are means with standard errors in parentheses
[a]0 = undisturbed, 1 = disturbed.
[b]1 = deeply flooded, 2 = shallowly flooded, 3 = rarely or never flooded.
[c]1 = moist to wet, 2 = dry.

Nutrient loading and processing

The mean concentration of TC in deposited sediment was 24.1 g C/kg of soil (SE = 1.6), TN was 1.5 g N/kg soil (SE = 0.1) and TP was 0.9 g P/kg soil (SE = 0.02). Sediment thickness was not statistically related to TOC ($p = 1.000$), TN ($p = 1.000$) or TP ($p = 0.810$). However, positive linear relationships ($p < 0.001$) existed between % silt + clay and TOC, TN and TP, and explained 21, 37 and 36% of the variation in these data sets, respectively. The mass of TN ($r^2 = 0.92$, $p < 0.001$) and TP ($r^2 = 0.64$, $p < 0.001$) in the deposited sediment were positively associated with the sediment organic fraction. The mean sediment C:N ratio was 20 (range 9–62, median = 18.6) and mean sediment C:P ratio was 27 (range 3–187, median = 24.8). Nutrient deposition was not correlated with sediment texture or thickness ($p > 0.8$) but was significantly ($p < 0.001$) higher at farther distances from the river ($r^2_{TN} = 0.35$; $r^2_{TC} = 0.24$; $r^2_{TP} = 0.43$).

Of the 181 resin bags retrieved, 40 were from plots where sediment accumulated and 141 were from plots without sediment deposition. Resin-$N_{inorganic}$ (resin-NO_3 + NH_4) was not significantly different ($p = 0.157$) between plots with (mean = 0.78 mg N/bag, SE = 0.21) and without (mean = 1.53 mg N/bag, SE = 0.48) sediment deposition. Plots with sediment had half the resin-PO_4 (mean = 0.05 mg P/bag, SE = 0.02, $p = 0.013$) of plots without sediment (mean = 0.12 mg P/bag, SE = 0.02). Resin bag nutrient content was not correlated with deposited sediment nutrient load ($p > 0.99$), thickness ($p > 0.99$) or texture ($p > 0.99$).

DISCUSSION

Heterogeneity of sediment deposition

The beaver dam complex we studied connected the Colorado River to its riparian zone (Westbrook *et al.*, 2006) resulting in ~750 m^3 of sediment deposition in a fragmented

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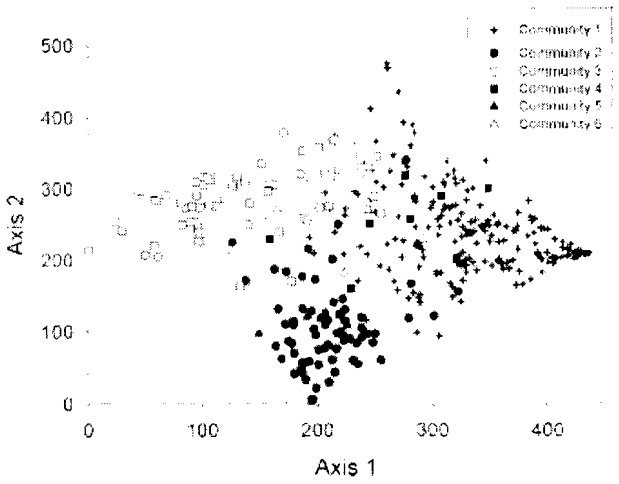

Figure 2. DCA ordination axes one and two scores for the plots overlain by indicator species of the plant communities defined through cluster analysis. Axis one represents a gradient of hydrologic condition following the flood created by beaver with deep water tables towards the left and shallow ones towards the right. Axis two represents a gradient of disturbance during the beaver flood where disturbance increases with decreasing ordination values

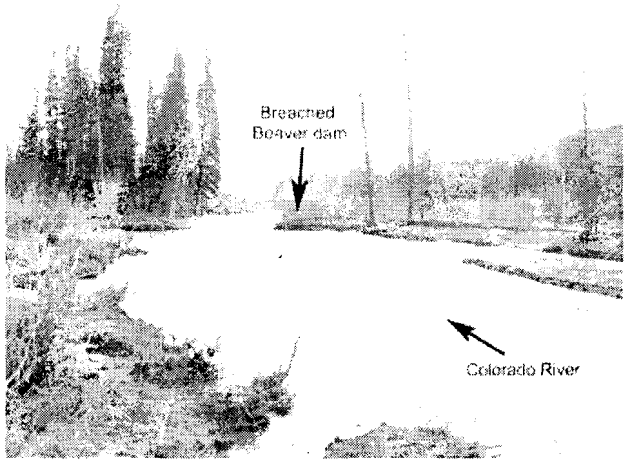

Figure 4. Photograph of the study area from 13 days following peak flow (11 June 2003) showing the breach dam site (from upstream) and the adjacent terrace upon which beaver driven flooding, sedimentation and sediment scouring occurred. Colorado River discharge at the time of the photo was ~21 $m^3 s^{-1}$ and the floodplain was inundated. This figure is available in colour online at wileyonlinelibrary.com

pattern on the floodplain and terrace during the dam's 6.5 year life. Sediment was likely transported across the floodplain by convective processes (Middelkoop and Asselman, 1998) in directions controlled by the floodwater pathways. The main flow vector was southwest across the valley bottom due to the valley slope, thus most sediment deposition occurred west of the river. The thickest sediment deposit (>1 m) occurred along the western flank of the dam likely because of the large reduction in shear stress (Nicholas and Walling, 1998) as stream energy was dissipated at the beaver dam (Gurnell, 1998). A reduction in sediment thickness with increasing distance from the river channel was expected (Middelkoop and Asselman, 1998; Kronvang and Falkum, 2002), but not found. The relatively uniform thickness with distance from the river channel may be attributed to the presence of beaver dams on the floodplain and terrace, which further decreased the velocity of moving water and increased its distribution and depth (Meentemeyer and Butler, 1999). The thickness of sediment deposited did, however, decline with increasing lateral distance from the main dam-diverted flow vector across the floodplain and terrace. Spatial heterogeneity in sediment deposition was also created by greater sediment deposition in less turbulent locations such as down-gradient of pre-dam plant hummocks, willow crowns or in topographic depressions. The beaver dam's effect on sediment deposition across the floodplain and terraces was more complex than predicted from 'ideal' patterns of sediment transport by turbulent diffusion (Bridge, 2003). Our findings were more consistent with Jeffries *et al.* (2003) who showed that the combination of an in-channel coarse woody debris dam, vegetation patterns and floodplain topography led to a spatially incoherent pattern of sediment deposition.

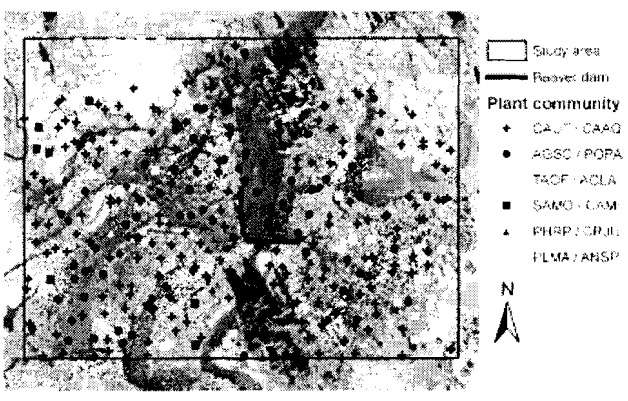

Figure 3. Air photograph of the study area (180 m × 240 m) showing different plant communities defined through cluster analysis. Indicator plants for each cluster are given as the first two letters from the genus and the first two letters of the species. The background image was flown on 9 September 2001 and shows the 'beaver flood' during baseflow conditions

Floodwaters on the terrace west of the river were detained by the construction of off-channel dams by beaver. These dams slowed water movement enough so that mineral sediment of even the finest grain sizes was deposited. Thus, our observations suggest the six small beaver dams slowed the velocity and increased the depth and areal distribution of water on the floodplain and terrace, which greatly magnified the ecological consequences of the single, large beaver dam built across the Colorado River.

In addition to sediment volume being spatially heterogeneous, sediment texture also varied throughout the study

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area. We found a strong gradient in sediment sand content from the floodplain to the terrace, as well as a gradient with increasing distance from main flow path across the terrace. The highest concentration of larger sediment grains occurred near the main channel, as is well known from overbank floods on most rivers (e.g. He and Walling, 1998). The percentage of fine grained sediments (silt + clay) east of the river was relatively homogenous, likely due to mixing by river turbulence when the beaver pond breached in one short, episodic event.

The volume of sediment deposited on the floodplain and terrace due to beaver driven flooding ($\sim$750 m^3) was relatively large for the Colorado River, which has a mean annual sediment yield of 15–6500 m^3 (assuming a bulk density of 2650 $kg\,m^{-3}$) and drains 165.5 km^2. Overbank sediment deposition during floods created by the Eurasian beaver (*Castor fiber*) has been documented for the River Jossa in Germany and deposits were considerably thinner (John and Klein, 2003). Deposition of sediment on floodplains during overbank floods may be expected, but often only very large floods are able to connect rivers to terraces. For the beaver flood we analysed, nearly all of the sediment was deposited on a terrace 0.7 to 1.2 m above the floodplain. It would take a flood with a return interval of at least 200 years, and probably > 500 years, to achieve a stream stage sufficient to connect the Colorado River to this terrace (Westbrook *et al.*, 2006). Beaver dams can place water and sediment on terraces located above the floodplain, and can dramatically increase the duration of flooding. Without beaver, snowmelt driven floods are typically short in duration, sometimes occurring before the growing season. In contrast, beaver dams can raise the water table throughout the year (Westbrook *et al.*, 2006), which can dramatically alter plant establishment and survival processes. Sediment deposited on the terrace is protected from future remobilization by overbank floods because the deposition areas are disconnected from the river unless beaver build another dam that reconnects them. Tall dams similar to the 1.7 m dam we studied are relatively common in areas with incised channels, although the maximum height of a beaver dam is structurally limited to 2.5 m (Dungmore, 1914; Townsend, 1953). Our findings indicate that a 'beaver flood' is an important and unique type of 'overbank flood', and suggest the terms 'floodplain' and 'terrace' need redefinition when describing rivers that commonly support beaver and have beaver-driven flood events.

Heterogeneity of vegetation

The distribution of plant communities following beaver abandonment was spatially heterogeneous and reflected the beaver influenced heterogeneity in the physical environment. Community composition was not associated with soil nutrient availability the year after the dam breach, which has been identified as a key controlling factor in other studies (Steed *et al.*, 2002; Wassen *et al.*, 2002; Wright *et al.*, 2002). Instead, plant community composition was influenced by the spatial pattern of sediment deposition and the hydrologic regime both during and following beaver occupation. These results contrast with studies performed in low order riverine environments, where beaver-created patches increase species richness at a landscape scale but are themselves fairly homogeneous units (Wright *et al.*, 2002). The high degree of heterogeneity we observed in a young beaver environment was likely due to differential degrees of sediment deposition and erosion. Different rates of sediment erosion can cause the development of different plant communities (McMaster and McMaster, 2000).

Here we present a simple conceptual model of how landforms and plant communities likely developed or were altered following beaver occupation, and the potential trajectories of key species and plant communities for our study site. Plant communities in areas lacking exposed mineral sediment were either: (1) relict upland plants that were not killed because the sites were not flooded or (2) newly formed wet meadows in sites periodically flooded during beaver occupation (indicator species *C. utriculata* and *C. aquatilis*). Plant communities in areas with sediment deposition either: (1) remained unaffected because they were located on hummocks; (2) formed on sediment that remained wet following the dam breach or (3) developed on sediment that dried out following the dam breach. We suggest that the term beaver meadow should be expanded to include all communities—herbaceous plant dominated wet and meadows, and willow-dominated communities—created on terraces by the effects of within-channel beaver dams.

Plants that colonized bare sediment influenced the successional trajectory of terraces. Willow and aspen seedlings were most commonly found in highly disturbed plots with wet or dry meadow plant communities in the summer following the dam breach. Willow established on bare, wet sediment the year of the dam breach, and survived even in sites that became dry meadows because as seedlings age they relied on groundwater rather than soil moisture (Karrenberg *et al.*, 2002). Historic air photos show that willow carr plant communities are common throughout the upper Colorado River valley (Westbrook, 2005). Many of our plots that contain willow seedlings will develop into willow-dominated communities where seedlings survive and grow. Willow patches are essential habitat for future beaver occupation as willow stems are the primary source of food and building material for beaver in the valley. Willow and aspen seedlings found in plots during 2004 were still alive in 2005 (C. Westbrook, personal observation), however, the long-term fate of these seedlings is uncertain. Elk browsing has drastically reduced the vigour of willow and other species in RMNP (Peinetti *et al.*, 2002; Baker *et al.*, 2005, Gage and Cooper, 2005). Intense ungulate

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herbivory may drive the former beaver-engineered willow carr community towards relatively dry meadows that persist as sedge- or grass-dominated patches unable to support beaver (Wolf *et al.*, 2007). Thus, the successional pathways in our system will likely be multidirectional and non-linear, as has been observed in other systems (e.g. Remillard *et al.*, 1987).

Nutrient availability

The total organic C, N and P deposited with sediment via transient sorption to sediment grains (Triska *et al.*, 1994) or as organo-complexes in the study area were approximately 102 kg C ha^{-1}, 7 kg N ha^{-1}, and 4 kg P ha^{-1}. The significant positive linear relationships of silt + clay with TOC, TN and TP are consistent with the theory of preferential association of nutrients with fine grained sediment particles; i.e. clay sized particles have large surface area and thus high cation exchange and microbial colonization capacities (Walling and He, 1994; Songster-Alpin and Klotz, 1995; Steiger and Gurnell, 2002). However, sediment texture explained relatively little of the variation (<37%) in nutrient content. This may be because the majority of sediment samples had high sand content. Alternatively, the variation in nutrient content is better explained by the percent TOC. Our results suggest that the amount of deposited organic matter, rather than the amount of mineral sediment, is the best predictor of sediment nutrient status, at least in this riverine system. This result contrasts the findings of Steiger and Gurnell (2002) who showed that the texture of the mineral fraction of deposited sediment controlled the amount of deposited TOC and total organic N.

Sediment C:N and C:P ratios were generally <20 and <200, respectively, which should promote net N and P mineralization. Drying of sediment after beaver dams are breached and floodplain water level decline can result in sequestration of bio-available N and P, which may be released upon re-wetting (Scholtz *et al.*, 2002) by overbank flows, rainfall or snowmelt. While the precipitation records show near average rainfall throughout the two summers following the beaver dam breach, nutrient availability was significantly lower in the newly deposited sediments than in the soils present prior to the beaver disturbance. Pinay and Naiman (1991) found enhanced N availability and cycling due to rapid shifts in the hydrologic condition adjacent to beaver flooded areas. The areas adjacent to those permanently flooded during the beaver occupation had a relatively dynamic hydrologic regime, i.e. a water table that was high during the snowmelt period and then declined over the summer. Such rapid shifts in hydrologic condition would lead one to believe nutrient availability would be greatest in these plots. In addition, plots with sediment deposition may have had relatively lower nutrient availability because of the strong relationships between percent TOC and sediment nutrient content. The organic matter may have been fairly recalcitrant as it was often laden with conifer needles. This would slow decomposition and associated nutrient release (Trumbore, 2000), meaning that it may take time for biogeochemical cycles to establish in the newly deposited sediment. Thus, the resin bag data from our study indicate there was no long-term alteration to soil N due to the beaver flood, which suggests the landforms created by beaver on the Colorado River terrace were unlike those created by beaver in boreal forests (Naiman and Melillo, 1984; Pinay and Naiman, 1991).

BEAVER INFLUENCED RIVER VALLEY FORMATION

The physical substrate for riparian shrubland formation is created by repeated and frequent hydrologic connection of a river to its floodplain, which creates the conditions necessary for mineral sediment erosion and deposition. Pioneer riparian plant species can colonize newly emergent landforms and spatial variation in hydrogeomorphic conditions is conducive for complex riparian vegetation community development (Naiman and Décamps, 1997; Ward *et al.*, 1999). The cumulative effects of these hydrogeomorphic processes over time lead to the formation of alluvial river valleys (Bridge, 2003).

Our results show how beaver drive key geomorphic processes in alluvial river valley formation, at least for streams of 5th order or smaller. These processes help explain how beaver dams can influence the spatial and temporal patterns across landscape scales. In our study, the current beaver population represented only 5% of the 600 beaver that were estimated to have been present in 1940 (Packard 1947; Mitchell *et al.*, 1999). However, abundant beaver in the past may have strongly influenced the formation of the Colorado River valley. The cycle of beaver colonization and abandonment of dams over time would form sediment patches that are spatially heterogeneous, overlap with other patches in time and space, and vertically layer on top of one another throughout the valley's floodplain and terrace. Existing theory and empirical evidence has been developed from riverine environments where the pond was the main hydrologic effect of beaver and sedimentation within the pond the main geomorphic signature of beaver meadow formation (Meentemeyer and Butler, 1999; Bigler *et al.*, 2001). Results presented herein demonstrate that in riverine environments where downstream flooding on floodplains and terraces is the main hydrologic effect of beaver (Westbrook *et al.*, 2006), sediment deposition and scouring on terraces is the main geomorphic signature of beaver meadow formation. By expanding existing beaver meadow theory beyond the beaver pond to include terraces within valley we more fully explain how beaver can help drive the formation of alluvial valleys and their complex vegetation

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patterns as was first postulated by Ruedemann and Schoonmaker in 1938.

CONCLUSIONS

This study documents a distinctly different mechanism of beaver meadow formation in riparian areas. An in-channel beaver dam triggered overbank flooding, killing vegetation in areas deeply flooded during the beaver occupation. Only vegetation on hummocks survived the deep flooding. Sediment accumulated on the floodplain and terrace along the water's flow path. The deposited sediment remained following the dam breach during the large flood, and was protected from future re-mobilization during snowmelt driven floods because the deposition areas were mainly on terraces. Many hydrologically connected areas did not accumulate sediment, rather vegetation was drowned by floodwaters. During and following the dam breach, vegetation was scoured exposing mineral soil and previously flooded areas were de-watered. Bare sediment and exposed soil was colonized by the clonal *Carex utriculata* and *C. aquatilis* on wet sites and new genets of *Agrostis scabra* and *Poa palustris* on dry sites, forming a complex beaver meadow. *Salix* spp. seedlings established on bare soil in these two communities, indicating that the beaver meadow may be dominated by tall shrubs in the future. Beaver create and interact with landscapes by processes not previously understood. We assert that the theory of beaver meadow formation should encompass the fundamentally distinct hydrogeomorphic processes that occur when beaver influence floodplains and terraces within large alluvial river valleys.

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