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Landscape-scale carbon storage associated with beaver dams

Ellen Wohl[1]

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[1] Beaver meadows form when beaver dams promote prolonged overbank flooding and floodplain retention of sediment and organic matter. Extensive beaver meadows form in broad, low-gradient valley segments upstream from glacial terminal moraines. Surveyed sediment volume and total organic carbon content in beaver meadows on the eastern side of Rocky Mountain National Park are extrapolated to create a first-order approximation of landscape-scale carbon storage in these meadows relative to adjacent uplands. Differences in total organic carbon between abandoned and active beaver meadows suggest that valley-bottom carbon storage has declined substantially as beaver have disappeared and meadows have dried. Relict beaver meadows represent ~8% of total carbon storage within the landscape, but the value was closer to 23% when beaver actively maintained wet meadows. These changes reflect the general magnitude of cumulative effects in heterotrophic respiration and organic matter oxidation associated with historical declines in beaver populations across the continent. **Citation:** Wohl, E. (2013), Landscape-scale carbon storage associated with beaver dams, *Geophys. Res. Lett.*, *40*, 3631–3636, doi:10.1002/grl.50710.

1. Introduction

[2] Beaver (*Castor canadensis* in North America and *C. fiber* in Europe) are ecosystem engineers [*Rosell et al.*, 2005] because of the diverse effects created by their construction of dams and canals along small- to medium-sized rivers [*Pollock et al.*, 2003]. Beaver dams obstruct flow, creating backwater areas that store sediment [*Butler and Malanson*, 1995; *Pollock et al.*, 2007] and organic matter [*Naiman et al.*, 1986, 1994]. Dams also enhance magnitude, duration, and frequency of overbank flow [*Westbrook et al.*, 2006]. Overbank flow forms stable, multithread channels [*John and Klein*, 2004; *Green and Westbrook*, 2009; *Polvi and Wohl*, 2012], floodplain deposition of fine sediment and organic matter [*Wohl et al.*, 2012], and high riparian water tables and floodplain wetlands [*Hood and Bayley*, 2008]. The resulting wet valley bottoms are known as beaver meadows [*Ruedemann and Schoonmaker*, 1938; *Ives*, 1942; *Westbrook et al.*, 2011]. Greater diversity of instream and floodplain habitats associated with beaver promotes greater biomass and biodiversity than valley segments not inhabited by beaver [*McDowell and Naiman*, 1986; *Wright*, 2009], as well as greater standing stocks and longer retention of nutrients [*Naiman et al.*, 1986, 1994; *Correll et al.*, 2000]. By reducing longitudinal river connectivity [*Burchsted et al.*, 2010] and enhancing lateral [*Westbrook et al.*, 2006] and vertical [*Briggs et al.*, 2012] river connectivity, beaver fundamentally alter river networks [*Naiman et al.*, 1988] and create alternative stable states [*Wolf et al.*, 2007; *Wohl*, 2013]. Areas with ideal habitat can support beaver populations for thousands of years [*Kramer et al.*, 2012; *Polvi and Wohl*, 2012].

[3] Most studies documenting physical and ecological effects of beaver meadows focus only on a few beaver colonies (*Johnston and Naiman* [1990] is an exception). Very few studies address the cumulative effects of widespread dam removal across North America and Europe over the past few centuries [*Pollock et al.*, 2003], despite the likelihood of substantial hydrologic, geomorphic, and biological cumulative effects. Sixty to 400 million beaver inhabited ~15 million km^2 of North America [*Naiman et al.*, 1988], for example, and substantial or complete reductions in beaver populations occurred following European settlement of the continent.

[4] I present landscape-scale estimates of cumulative sediment and organic carbon storage associated with beaver dams in mountainous headwater catchments within Rocky Mountain National Park (RMNP) in Colorado, USA, as an example of the regional assessments necessary to understand the cumulative effects of reduced beaver populations. I use detailed characterizations of two headwater catchments and reconnaissance-level surveys of the extent of beaver dams in an additional 25 catchments to infer regional cumulative effects of dam removal associated with 19th and 20th century declines in beaver populations. In headwater catchments of the U.S. Rocky Mountains, the greatest beaver-enhanced aggradation occurs in low-gradient valleys and depressions of glacial origin [*Persico and Meyer*, 2009]. As much as half of the postglacial sediment in such areas is associated with beaver dams [*Kramer et al.*, 2012; *Polvi and Wohl*, 2012], and high percentages of organic carbon, along with greater sediment volume per unit length of valley, result in beaver meadows disproportionately serving as carbon sinks within mountainous river networks [*Wohl et al.*, 2012].

2. Study Area

[5] The study area is the eastern side of Rocky Mountain National Park (RMNP). Beaver were historically present in RMNP from the highest portions of the subalpine conifer forest zone (3400–2740 m) down to and beyond the lowest elevations within the park [*Packard*, 1947]. Valley and channel geometries in the region exhibit substantial longitudinal variability, with predominantly steep, narrow valley segments and limited broad, low-gradient valley segments (here referred to as unconfined). Most channel segments have a single-thread planform, but a stable multithread planform can occur within unconfined valleys where logjams or beaver

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[1]Department of Geosciences, Colorado State University, Fort Collins, Colorado, USA.

Corresponding author: E. Wohl, Department of Geosciences, Colorado State University, Fort Collins, CO 80523-1482, USA. (ellen.wohl@colostate.edu)

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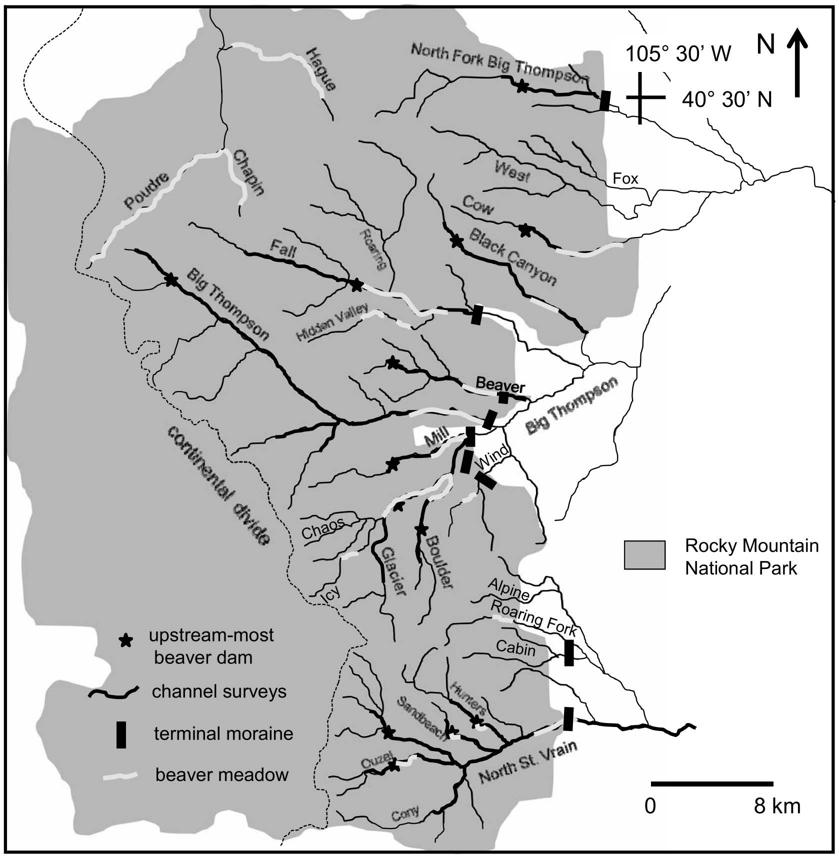

Figure 1. Location map of the study sites in Rocky Mountain National Park, Colorado. Upper Beaver Meadows is the beaver meadow indicated on Beaver Brook. The surveyed reach along the Poudre River extends from the start of the beaver meadow to the junction with Chapin Creek.

dams obstruct flow and create backwaters that facilitate sedimentation, overbank flow, and formation of secondary channels [*Wohl*, 2011, 2013].

[6] The most extensive and well-developed multithread channel segments occur in unconfined valleys immediately upstream from glacial terminal moraines (Figure 1). I refer to these as extensive beaver meadows. RMNP was glaciated multiple times during the Pleistocene, with glaciers extending down to ~2300–2400 m elevation. Terminal moraines raised local base levels and facilitated accumulation of outwash sediment and formation of relatively broad, low-gradient valley segments during glacial retreat. Beaver subsequently colonized these valley segments, in which the broad valley bottom maximizes ponded and overbank deposition associated with beaver dams. Ground penetrating radar (GPR) surveys of Upper Beaver Meadows, a broad valley segment immediately upstream from the moraine that affects Beaver Brook, indicate maximum postglacial sediment thicknesses of 6 m, with an average of 1.3 m. As much as half of this sediment is associated with beaver dams [*Kramer et al.*, 2012].

[7] Beaver-related sedimentation depends on riverine scale. Smaller streams along which dams persist longer have more pond deposition, whereas beaver dams primarily enhance overbank deposition along larger streams, which have more frequent dam failure [*Levine and Meyer*, 2013]. The streams examined in RMNP are relatively small streams (<10 m wide) in wide valleys along which beaver dams promote both ponded and floodplain deposition. I refer to all beaver-induced deposition as beaver sediment.

[8] Beaver populations partly recovered from early 19th century trapping, reaching a maximum within RMNP circa 1940, before declining again, particularly after circa 1980 [*Kramer*, 2011]. Although there may be multiple reasons for the decline, intensive grazing by elk (*Cervus canadensis*) of woody riparian vegetation may be partially responsible by limiting food and dam-building materials for beaver. Elk numbers within RMNP have climbed since wolves were hunted to extinction in the region during the 1920s, although park managers have tried to manage the elk population since the 1930s [*Hess*, 1993]. Evidence for much more widespread beaver activity in the past remains in the form of relict, breached dams and ponds filled with fine-grained, organic-rich sediments. Data collection focused on Beaver Brook and the upper Poudre River (Figure 1 and Table S1 in the supporting information). A 1947 survey of beaver populations in RMNP recorded numerous beaver at these sites [*Packard*, 1947]. No beaver were present at either site by the time of the next survey in 1999 [*Mitchell et al.*, 1999].

3. Methods

[9] Field methods included longitudinally continuous channel surveys to map relict beaver dams and sediment. Although this study emphasizes Beaver Brook and the upper Poudre River, I mapped the location of relict beaver dams and beaver on an additional 13 drainages on the eastern side of RMNP during 2010 and 2011 (Figure 1). Features were mapped using a handheld GPS with horizontal resolution of ±3 m. Channel

Table 1. Calculated Values for the Entire Data Set of 27 Watersheds

			Beaver Meadows[b]							
River	Dr A[a] (km^2)	Total Length (m)	Length (m)	Proportion[c]	W_m[d] (m)	W_a[e] (m)	Total Vol (m^3)	Beaver Sed Vol[f] (m^3)	TOC[g] (Mg)	TOC[h] (Mg)
NF Big Thompson River	30.3	13,150	0	–	–	–	–	–	–	–
Fox Creek	7.8	5,015	0	–	–	–	–	–	–	–
West Creek	30.0	10,915	0	–	–	–	–	–	–	–
Cow Creek	20.0	8,425	2,090	0.25	110	100	271,700	135,850	8,070	29,344
Black Canyon Creek	19.2	11,530	920	0.08	100	80	95,680	47,840	2,842	10,333
Roaring River	32.5	11,365	0	–	–	–	–	–	–	–
Icy Brook	7.7	3,880	410	0.11	185	100	53,300	26,650	1,583	5,756
Chaos Creek	8.9	4,610	0	–	–	–	–	–	–	–
Wind River	11.6	5,395	780	0.14	130	100	101,400	50,700	3,012	10,951
Alpine Brook	5.1	4,290	0	–	–	–	–	–	–	–
Roaring Fork Creek	5.4	6,810	390	0.06	145	100	50,700	25,350	1,506	5,476
Cabin Creek	5.7	5,020	0	–	–	–	–	–	–	–
Hunters Creek	12.5	8,210	340	0.04	100	80	35,360	17,680	1,050	3,819
Sandbeach Creek	3.8	5,165	380	0.07	220	150	74,100	37,050	2,201	8,003
Ouzel Creek	14.1	8,755	1,860	0.21	120	100	241,800	120,900	7,182	26,114
Cony Creek	19.9	9,150	0	–	–	–	–	–	–	–
Fall River[i]	90.3	16,555	5,920	0.36	935	520	4,001,920	2,000,960	118,856	432,207
Hidden Valley Creek	11.4	4,140	3,330	0.80	370	230	995,670	497,835	29,571	107,532
Beaver Brook	21.6	9,120	4,710	0.52	500	350	2,143,050	1,071,525	63,647	231,449
Big Thompson River	110.8	23,160	6,020	0.26	1080	920	7,100,020	3,599,960	213,837	777,591
Mill Creek	15.4	12,085	4,110	0.34	330	200	1,068,600	534,300	31,737	115,409
Glacier Creek	52.8	14,090	4,360	0.31	690	380	2,153,840	1,076,920	63,967	232,615
Boulder Brook	12.9	9,600	2,390	0.25	700	490	1,522,430	761,215	45,213	164,422
N St. Vrain Creek	88.9	12,940	900	0.07	470	380	444,600	222,300	13,205	48,017
Upper Poudre River	21.5	15,590	12,810	0.82	90	40	666,120	333,060	19,784	71,941
Hague Creek	37.8	12,520	7,290	0.58	305	240	2,274,480	1,137,240	67,551	245,644
Chapin Creek	19.5	4,570	3,660	0.80	420	290	1,379,820	689,910	40,979	149,021
cumulative	717.4	256,055	62,670	0.24[j]			24,774,490	12,387,245	735,801	2,675,645

[a]Drainage area at eastern boundary of RMNP, or mouth of stream, whichever comes first proceeding downstream.
[b]All values are for valley length within the boundaries of RMNP; drainages with "0" for length do not have beaver meadows.
[c]Refers to the proportion of the total channel length in beaver meadows (ratio of preceding two columns); where a terminal moraine is present, the beaver meadow is longitudinally continuous and all influenced by the terminal moraine.
[d]Maximum valley-bottom width in the beaver meadows.
[e]Average valley-bottom width in the beaver meadows.
[f]Half of total sediment volume in previous column.
[g]Total organic carbon, using average value of 3.3%.
[h]Total organic carbon, using average value of 12%.
[i]Italics indicate catchment where beaver meadows are influenced by position of glacial moraine.
[j]Average value.

surveys began close to treeline and continued downstream to the park boundary. Some large beaver meadows continue farther downstream, but this boundary provides a consistent, readily identifiable stopping point. I supplemented this data set with 12 additional drainages on the eastern side of the park for which I could identify the presence of extensive beaver meadows using topographic maps and aerial photographs. I delineated the length and width of each beaver meadow, assumed a depth of 1.3 m of fine-grained sediment based on GPR data from Beaver Brook meadow [*Kramer et al.*, 2012], and calculated the total volume of stored sediment (see supporting information). Based on the GPR surveys and interpretations from the Beaver Brook meadow [*Kramer et al.*, 2012], I conservatively assumed that half of the total volume of sediment was beaver related. The complete data set thus includes 27 streams.

[10] Detailed surveys of Beaver Brook and the upper Poudre River form the intensive data set. Relict beaver dams in steep, narrow channel segments were identified based on geometry and vegetation (supporting information), and the sediment volume was estimated for each dam. The data set included 148 dams along Beaver Brook and 100 dams along the upper Poudre River, as well as an extensive beaver meadow along each channel.

[11] I sampled and analyzed beaver sediment for total organic carbon (TOC) analysis (supporting information). Fifteen samples of beaver sediment from Beaver Brook and 14 samples from the Upper Poudre River were collected and analyzed for total organic carbon (TOC) (supporting information). These 29 samples were in addition to 10 TOC samples of the Beaver Brook meadow from an earlier study, as well as 19 samples from active beaver meadows in RMNP [*Wohl et al.*, 2012]. I estimated the magnitude of stored organic carbon using the average TOC content of all samples, an average bulk density of 1.8 g/cm^3 for beaver sediment [*Wohl et al.*, 2012], and the volume of beaver sediment.

4. Results

[12] The largest estimated volumes of beaver sediment occur in extensive beaver meadows along rivers influenced by terminal glacial moraines (Table 1 and Figure S3 in the supporting information). Although individual relict beaver dams extend most of the channel length on Beaver Brook, 95% of the total beaver sediment occurs within the large beaver meadow near the moraine (Table S1 and Figure S4 in the supporting information). These proportions provide a rationale for estimating the landscape-scale storage of beaver sediment using only beaver meadows. Extensive beaver meadows occupy approximately a quarter of the total length of primary valleys on the eastern side of RMNP (Table 1).

[13] Using an average value of 3.3% TOC for beaver sediment in relict beaver meadows (Table S2 in the supporting information), ~735,800 Mg of organic carbon is stored in beaver meadows. In relict beaver meadows, riparian water tables have dropped, floodplain deposition of organic matter has declined, and carbon has been lost through drying and oxidation [*Naiman et al.*, 1994; *Trumbore and Czimczik*, 2008]). Upland forest soils in the region average 7.3% TOC [*Rueth and Baron*, 2002]. Based on samples collected from active beaver meadows, I used an average TOC value of 12% [*Wohl et al.*, 2012] to estimate the TOC storage when beaver meadows were active. Assuming that all beaver meadows were active simultaneously results in ~2,675,645 Mg of organic carbon storage.

[14] To compare these values to the total estimated organic carbon stored in the data set of 27 watersheds, I used the total drainage area of 717 km^2 with published values of 260 Mg C/ha ecosystem carbon stock in forested uplands [*Bradford et al.*, 2008] and 105 Mg/ha in tundra uplands [*Hartman et al.*, 2009] in the region. Proportions of land cover within the Fall River, Big Thompson, and North St. Vrain Creek within RMNP average 0.33 unvegetated, 0.23 tundra, 0.39 forest, and 0.05 subalpine meadow, with relatively little variation between drainages [*Clow and Sueker*, 2000]). I extrapolated these land cover values to the data set of 27 watersheds and estimated 9,012,500 Mg of C in the uplands. The estimated contemporary carbon storage (average 3% TOC) in beaver meadows thus represents ~8% of the total carbon storage in the landscape. The former carbon storage when these beaver meadows were active (average 12% TOC), prior to abandonment and drying, represents ~23% of the landscape total.

5. Discussion

[15] The estimates of TOC stored in beaver meadows on the eastern side of RMNP represent a first-order approximation for several reasons, as detailed in the supporting information, including use of single average values for thickness of beaver sediment, soil bulk density, and percent soil TOC. Similarly, the estimated change in total carbon storage by a factor of more than three from the last period of active beaver meadows to the present is a first-order approximation. Each set of TOC samples includes substantial variation (Figure S5 in the supporting information), as do published values of upland carbon. The estimated mean values of TOC for the two populations of active and abandoned beaver meadows are consistent across multiple sampling sites, however, and differ significantly from one another.

[16] Although values of carbon storage can be refined, the trends indicated in this analysis are robust: beaver meadows store the great majority of carbon along rivers in these mountainous headwater catchments; this source of carbon storage cumulatively represents ~8% (relict) to 23% (active) of estimated total landscape carbon storage; and riverine carbon storage has declined substantially with the replacement of beaver meadows with drier “elk grasslands” [*Wolf et al.*, 2007]. The estimated 23% of total landscape carbon storage within active beaver meadows also agrees well with an earlier estimate of 25% of total carbon storage in unconfined valley bottoms that included beaver meadows and old-growth forest with substantial downed wood [*Wohl et al.*, 2012].

[17] Estimated total carbon storage during periods of active beaver meadows does not imply that all of the extensive meadows were continuously occupied during the Holocene. Although these sites represent optimal beaver habitat, they may all have been simultaneously occupied only during cooler, wetter intervals of the Holocene [*Persico and Meyer*, 2009, 2013]. The estimated carbon storage using 12% TOC and total sediment volume in extensive beaver meadows represents maximum potential carbon storage at the landscape level relative to contemporary, relatively low values. These low contemporary values may reflect some combination of elk competition, progressively warmer and drier late 20th century climate [*Westerling et al.*, 2006], and other factors that limit beaver populations in the study area.

[18] These results illustrate the importance of beaver meadows at the landscape scale. In addition to site-specific changes well documented in the literature, ecosystem engineering by beaver results in significant landscape-scale storage of carbon. Restoration of beaver populations and beaver meadows thus assumes critical importance in headwater management strategies designed to enhance ecosystem services such as habitat provision and carbon sequestration. When beaver are removed, wet beaver meadows are replaced by the alternate stable state of relatively dry grasslands [*Wolf et al.*, 2007; *Green and Westbrook*, 2009; *Polvi and Wohl*, 2012]. Dry grassland soils average 40–100 Mg C/ha [*Buringh*, 1984], as opposed to the values of 300–400 Mg C/ha in relict beaver meadows and 1150–1400 Mg C/ha in active beaver meadows estimated in this study.

[19] This valley-bottom metamorphosis likely has important implications for ecosystem resilience to climate change, drought, and wildfire. Beaver populations and their dam-induced hydrologic effects have varied during the Holocene in response to climate fluctuations [*Persico and Meyer*, 2009, 2013] and will presumably vary in future. The persistence of at least some beaver, however, and the maintenance of higher riparian water tables probably created Holocene refugia for more mesic communities during drier intervals. The buffering effects of wet valley bottoms during brief, episodic disturbances are illustrated by the 2012 Fern Lake Fire in RMNP, which burned a substantial portion of Moraine Park along the Big Thompson River. Moraine Park was an active beaver meadow into the 1960s [*Polvi and Wohl*, 2012], and the wet valley bottom had not burned prior to the 2012 fire, despite several historical fires in the catchment.

6. Conclusions

[20] The recent loss of beaver populations in mountainous headwater catchments in Rocky Mountain National Park in Colorado, USA, provides an opportunity to examine large-scale implications of older historical loss or reduction of beaver populations throughout Eurasia and North America. Absence of beaver and beaver dams drives the metamorphosis of wide valley-bottom segments from wet beaver meadows to drier grasslands, with associated loss of habitat, biodiversity, and carbon storage. First-order approximations of total carbon storage on the eastern side of RMNP suggest that the volume of organic carbon stored in beaver meadows represents 8 to 23% of the estimated total carbon storage across 27 watersheds. Estimated cumulative carbon storage in beaver meadows decreased by a factor of more than three with loss of beaver populations. Widespread alteration of unconfined valley segments in these mountainous headwater stream networks provides a starting point to understand the magnitude of cumulative effects associated with historical declines in beaver populations across headwater and lowland stream networks.

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References

Bradford, J. B., R. A. Birdsey, L. A. Joyce, and M. G. Ryan (2008), Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests, *Glob. Chang. Biol.*, *14*, 2882–2897.

Briggs, M. A., L. K. Lautz, J. M. McKenzie, R. P. Gordon, and D. K. Hare (2012), Using high-resolution distributed temperature sensing to quantify spatial and temporal variability in vertical hyporheic flux, *Water Resour. Res.*, *48*, W02527, doi:10.1029/2011WR011227.

Burchsted, D., M. Daniels, R. Thorson, and J. Vokoun (2010), The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters, *Bioscience*, *60*, 908–922.

Buringh, P. (1984), Organic carbon soils of the world, in *The role of terrestrial vegetation in the global carbon cycle*, edited by G.M. Woodwell, pp. 91–109, John Wiley and Sons, Chichester, UK.

Butler, D. R., and G. P. Malanson (1995), Sedimentation rates and patterns in beaver ponds in a mountain environment, *Geomorphologie*, *13*, 255–269.

Clow, D. W., and J. K. Sueker (2000), Relations between basin characteristics and stream water chemistry in alpine/subalpine basins in Rocky Mountain National Park, Colorado, *Water Resour. Res.*, *36*, 49–61.

Correll, D. L., T. E. Jordan, and D. E. Weller (2000), Beaver pond biogeochemical effects in the Maryland coastal plain, *Biogeochemistry*, *49*, 217–239.

Green, K. C., and C. J. Westbrook (2009), Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams, *BC J. Ecosyst. Manage.*, *10*, 68–79.

Hartman, M. D., et al. (2009), DayCent-Chem simulations of ecological and biogeochemical processes of eight mountain ecosystems in the United States, U.S. Geological Survey Scientific Investigations Report, 2009–5150, 174 p.

Hess, K. (1993), *Rocky Times in Rocky Mountain National Park: An Unnatural History*, University Press of Colorado, Niwot.

Hood, G. A., and S. E. Bayley (2008), Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada, *Biol. Conserv.*, *141*, 556–567.

Ives, R. L. (1942), The beaver-meadow complex, *J. Geomorphol.*, *5*, 191–203.

John, S., and A. Klein (2004), Hydrogeomorphic effects of beaver dams on floodplain morphology: avulsion processes and sediment fluxes in upland valley floors (Spessart, Germany), *Quaternary*, *15*, 219–231.

Johnston, C. A., and R. J. Naiman (1990), The use of a geographic information system to analyze long-term landscape alteration by beaver, *Landsc. Ecol.*, *4*, 5–19.

Kramer, N. (2011), *An investigation into beaver-induced Holocene sedimentation using ground penetrating radar and seismic refraction: Beaver Meadows, Rocky Mountain National Park*, M.Sc. Thesis, Colorado State University, Fort Collins, Colorado.

Kramer, N., E. E. Wohl, and D. L. Harry (2012), Using ground penetrating radar to 'unearth' buried beaver dams, *Geology*, *40*, 43–46.

Levine, R., and G. A. Meyer (2013), Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA, *Geomorphology*, doi:10.1016/j.geomorph.2013.04.035, in press.

McDowell, D. M., and R. J. Naiman (1986), Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*), *Oecologia*, *68*, 481–489.

Mitchell, D. J., Tjornehoj, and B. Baker (1999), Beaver populations and possible limiting factors in Rocky Mountain National Park. Technical report, U.S. Geological Survey, Midcontinent Ecological Science Center.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie (1986), Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*), *Ecology*, *67*, 1254–1269.

Naiman, R. J., C. A. Johnston, and J. C. Kelley (1988), Alteration of North American streams by beaver, *Bioscience*, *38*, 753–762.

Naiman, R. J., G. Pinay, C. A. Johnston, and J. Pastor (1994), Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks, *Ecology*, *75*, 905–921.

Packard, F. M. (1947), A survey of the beaver population of Rocky Mountain National Park, Colorado, *J. Mammal.*, *28*, 219–227.

Persico, L., and G. A. Meyer (2009), Holocene beaver damming, fluvial geomorphology, and climate in Yellowstone National Park, Wyoming, *Quat. Res.*, *71*, 340–353.

Persico, L. P., and G. A. Meyer (2013), Natural and historical variability in fluvial processes, beaver activity, and climate in the Greater Yellowstone Ecosystem, *Earth Surf. Processes Landforms*, *38*, 728–750.

Pollock, M. M., M. Heim, and D. Werner (2003), Hydrologic and geomorphic effects of beaver dams and their influence on fishes, in *The Ecology and Management of Wood in World Rivers, American Fisheries Society Symposium 37*, edited by S.V. Gregory, K. Boyer, and A. Gurnell, pp. 213–233, American Fisheries Society, Bethesda, Maryland.

Pollock, M. M., T. J. Beechie, and C. E. Jordan (2007), Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon, *Earth Surf. Processes Landforms*, *32*, 1174–1185.

Polvi, L. E., and E. Wohl (2012), The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development, *Earth Surf. Processes Landforms*, *37*, 332–346.

Rosell, F., O. Bozsér, P. Collen, and H. Parker (2005), Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems, *Mammal Rev.*, *35*, 248–276.

Ruedemann, R., and W. J. Schoonmaker (1938), Beaver-dams as geologic agents, *Science*, *88*, 523–525.

Rueth, H. M., and J. A. Baron (2002), Differences in Engelmann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA, *Ecosystems*, *5*, 45–57.

Trumbore, S. E., and C. I. Czimczik (2008), An uncertain future for soil carbon, *Science*, *321*, 1455–1456.

Westbrook, C. J., D. J. Cooper, and B. W. Baker (2006), Beaver dam and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area, *Water Resour. Res.*, *42*, W06404, doi:10.1029/2005WR004560.

Westbrook, C. J., D. J. Cooper, and B. W. Baker (2011), Beaver assisted river valley formation, *River Res. Appl.*, *27*, 247–256.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam (2006), Warming and earlier spring increase western U.S. forest wildfire activity, *Science*, *313*, 940–943.

Wohl, E. (2011), Threshold-induced complex behavior of wood in mountain streams, *Geology*, *39*, 587–590.

Wohl, E. (2013), The complexity of the real world in the context of the field tradition in geomorphology, *Geomorphology*, doi:10.1016/j.geomorph.2012.12.016, in press.

Wohl, E., K. Dwire, N. Sutfin, L. Polvi, and R. Bazan (2012), Mechanisms of carbon storage in mountainous headwater rivers, *Nat. Commun.*, *3*, 1263, doi:10.1038/ncomms2274.

Wolf, E. C., D. J. Cooper, and N. T. Hobbs (2007), Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park, *Ecol. Appl.*, *17*, 1572–1587.

Wright, J. P. (2009), Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer, *Ecology*, *90*, 3418–3429.