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The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors

DeAnna Laurel and Ellen Wohl*
Department of Geosciences, Colorado State University, Fort Collins, CO USA

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*Correspondence to: Ellen Wohl, Department of Geosciences, Colorado State University, Fort Collins, CO 80523-1482, USA. E-mail: ellen.wohl@colostate.edu

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ABSTRACT: Beavers are widely recognized as ecosystem engineers for their ability to shape river corridors by building dams, digging small canals, and altering riparian vegetation. Through these activities, beavers create beaver meadows, which are segments of river corridor characterized by high geomorphic heterogeneity, attenuation of downstream fluxes, and biodiversity. We examine seven beaver meadows on the eastern side of the Rocky Mountain National Park, Colorado, USA with differing levels of beaver activity. We divide these sites into the four categories of active, partially active, recently abandoned (< 20 years), and long abandoned (> 30 years). We characterize geomorphic units within the river corridor and calculate metrics of surface geomorphic heterogeneity relative to category of beaver activity. We also use measures of subsurface geomorphic heterogeneity (soil moisture, soil depth, percent clay content, organic carbon concentration) to compare heterogeneity across beaver meadow categories. Finally, we calculate organic carbon stock within the upper 1.5 m of each meadow and compare these values to category of beaver activity. We find that surface geomorphic heterogeneity and mean soil moisture differ significantly only between active and long abandoned meadows, suggesting a non-linear decrease with time following beaver abandonment of a meadow. Soil depth and organic carbon stock do not differ consistently in relation to category of beaver meadow, suggesting that larger-scale geologic controls that foster deep floodplain soils can continue to maintain substantial organic carbon stocks after beavers abandon a meadow. These results also indicate that the effects of beaver ecosystem engineering can persist for nearly three decades after the animals largely abandon a river corridor. © 2018 John Wiley & Sons, Ltd.

KEYWORDS: beaver meadow; floodplain; wetlands; organic carbon; connectivity

Introduction

Beavers – *Castor canadensis* in North America and *Castor fiber* in Eurasia – are commonly referred to as an ecosystem engineer because of their ability to shape the physical environment and associated hydrologic, geomorphic, biogeochemical, and ecological processes of river corridors (Ruedemann and Schoonmaker, 1938; Guegan *et al.,* 1998; Beisel *et al.,* 2000; Wright *et al.,* 2002; Rosell *et al.,* 2005; Wright, 2009). River corridors include the channel (s), floodplain and riparian zone, and underlying hyporheic zone (Harvey and Gooseff, 2015). Where beavers have modified the channel (s) and floodplain over a period of years to decades, a spatial mosaic of active and abandoned dams and ponds and secondary channels known as a beaver meadow (Polvi and Wohl, 2012) develops. Here, we examine correlations between beaver activity, geomorphic heterogeneity, and organic carbon (OC) storage in river corridors of the Southern Rocky Mountains. We define surface geomorphic heterogeneity as the spatial diversity of geomorphic units characterized via morphology, elevation, and vegetation. We define subsurface geomorphic heterogeneity as the spatial diversity of soil moisture, depth, percent clay, and OC concentration. Examining correlations between beaver activity and river corridor form and function is important to understanding how river corridors have changed during the past few centuries as human activities have significantly reduced beaver population densities throughout the northern hemisphere.

Beavers engage in three primary activities that influence geomorphic heterogeneity and retention of water, sediment, and organic matter in flux along river corridors: building dams, digging narrow canals to facilitate their movements, and altering riparian vegetation via herbivory. Beaver dams can cross a main channel, secondary channels, floodplain channels, tributaries, or valley-side seeps and springs (Olson and Hubert, 1994; Johnston, 2012). Dams create areas of ponded water and enhance lateral connectivity between the channel and floodplain by increasing overbank flow (Westbrook *et al.,* 2006; Wegener *et al.,* 2017). Increased water surface area and higher riparian water table can also increase the resilience of the river corridor to disturbances including flood, drought, and wildfire (Hood and Bayley, 2008). By creating pressure gradients within the flow, dams increase vertical connectivity between the channel and hyporheic zone (Lautz *et al.,* 2006; Westbrook *et al.,* 2013). Dams can also attenuate downstream fluxes of water, sediment, solutes, and particulate organic matter (Naiman *et al.,* 1986, 1994; Butler and Malanson, 1995; Correll *et al.,* 2000; Wegener *et al.,* 2017). Canals dug by beavers can enlarge to become secondary channels and contribute to the formation of an anastomosing channel planform, which is commonly present where multiple beaver dams exist (John and Klein, 2004; Polvi and Wohl, 2012, 2013). Distribution of water among multiple channels reduces flow energy and enhances attenuation of flood peaks and retention of dissolved and particulate material. Finally, beaver herbivory can alter floodplain vegetation by favoring woody plants such as willows (*Salix* spp.) (Baker *et al.,* 2005; Veraart *et al.,* 2006). By facilitating the persistence of densely growing deciduous woody species in floodplains, beavers indirectly increase the hydraulic resistance of the floodplain by increasing overbank roughness and cohesion of floodplain sediment (Baker *et al.,* 2005).

In summary, the net effects of beaver activities are to make river corridors more geomorphically heterogeneous (Gurnell, 1998; Westbrook *et al.,* 2011; Polvi and Wohl, 2012; Westbrook *et al.,* 2013). Geomorphic heterogeneity in turn correlates with greater retention of materials in flux (e.g. Wohl *et al.,* 2012; Johnston, 2014; Wegener *et al.,* 2017); greater lateral (channel–floodplain) (Westbrook *et al.,* 2006) and vertical (channel–hyporheic) connectivity (Lautz *et al.,* 2006); and greater resilience to natural and human disturbance (Hood and Bayley, 2008). This understanding is critical in the context of the massive historical declines in beaver populations and associated metamorphoses of river corridors (Naiman *et al.,* 1988; Polvi and Wohl, 2013).

In regions such as some US national parks, beavers were once actively trapped, then subsequently protected, but are still declining because of competition from native ungulates and removal of ungulate-predators such as wolves (Ripple and Beschta, 2003; Wolf *et al.,* 2007; Beschta and Ripple, 2012). Loss of beavers and beaver dams commonly results in concentration of surface flow in a single channel, which is likely to incise. Overgrazing of deciduous woody species, abandonment of secondary channels, and incision of the main channel can lower the alluvial aquifer, transforming the river corridor into a so-called elk grassland (Peinetti *et al.,* 2002; Wolf *et al.,* 2007). An elk grassland is drier, less geomorphically heterogeneous, less retentive, and less resilient than a beaver meadow. We focus on the Rocky Mountain National Park (RMNP) in Colorado, USA, where the scenario described earlier has changed most of the former beaver meadows to elk grasslands.

Figure 1 illustrates the conceptual model underlying our work. The alternative states of an active beaver meadow (upper feedback loop) and a long abandoned beaver meadow, also known as an elk grassland (lower feedback loop), exhibit substantial differences in surface geomorphic heterogeneity. In this paper, we examine whether these two end-members are separated by an abrupt threshold, such that a beaver meadow rapidly becomes an elk grassland following beaver abandonment and the presence of beavers rapidly creates a beaver meadow. Alternatively, sites with differing levels of beaver activity and time since beaver abandonment could form a gradient with transitional levels of geomorphic heterogeneity, as indicated by the smaller feedback loops between the end-members. We focus on how beaver-induced geomorphic heterogeneity and retention of OC decrease with time once beaver activity declines or ceases at a site.

We hypothesize that geomorphic heterogeneity decreases non-linearly with time since beaver abandonment (Hypothesis 1, H1). Although observations from various river corridors clearly suggest loss of geomorphic heterogeneity following beaver abandonment (e.g. Green and Westbrook, 2009), we are not aware of any quantitative analyses of the relative

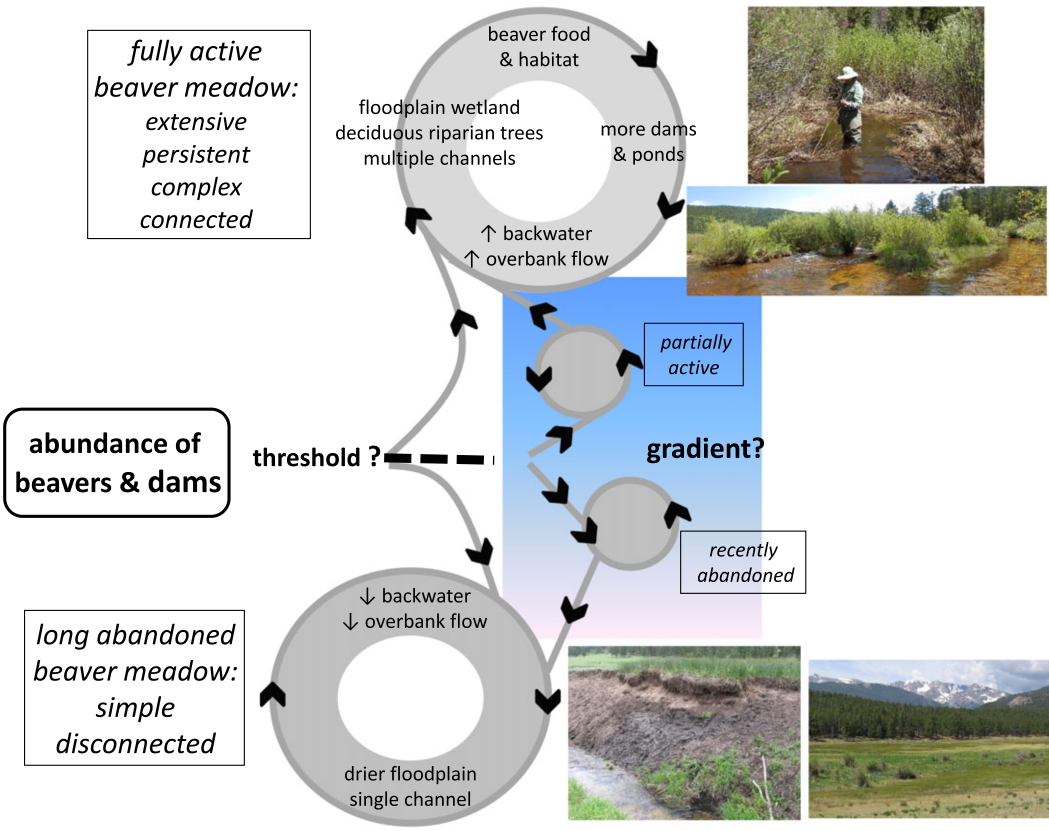

Figure 1. Conceptual model of feedbacks that maintain different configurations of a river corridor in the presence and absence of beaver. [Colour figure can be viewed at wileyonlinelibrary.com]

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rates at which these changes occur through time. We hypothesize a non-linear decrease with time because observations suggest that willows and secondary channels disappear within two to three decades of beaver abandonment, but the meadow then appears to undergo little additional change.

We also hypothesize that OC stock within floodplain soil declines non-linearly with time following beaver abandonment of a river corridor; specifically, we hypothesize an initial decline and then relative stability (Hypothesis 2, H2). We posit that the floodplain soils continue to store substantial quantities of OC, although these may be lower than stocks in active beaver meadows (Wohl, 2013). This hypothesis is based on observations that channel–floodplain connectivity is reduced as beaver abandon a site. This results in a declining riparian water table, so that floodplain soils are less likely to be saturated and maintain the reducing conditions that favor high OC concentrations (Trumbore and Czimczik, 2008). As riparian woody vegetation is replaced by herbaceous vegetation and grasses characteristic of shortgrass prairie, primary productivity and litterfall carbon inputs to the floodplain soil likely decline (Buell and Markewich, 2004). Peak flows are less likely to overtop the channel banks and add fluvially transported organic matter to the floodplain soil. All of these changes likely result in lower soil OC concentrations in abandoned beaver meadows, but if these changes occur within one to two decades following beaver abandonment and the valley bottom then becomes relatively stable (i.e. incised channel with minimal lateral migration), we expect floodplain soil carbon stocks to initially decline and then remain stable with time.

Study Area

We collected data in seven valley bottom meadows within the RMNP in north-central Colorado (Figure 2). RMNP is underlain by Precambrian crystalline rocks composed of granite, granodiorite, schist, and gneiss (Braddock and Cole, 1990), which produce sediment that is very low in calcium carbonate ($CaCO_3$) (Sutfin and Wohl, 2017). The eastern side of the park, where the meadows are located, is characterized by the high peaks of the continental divide, from which eastward-flowing streams descend along steep, narrow canyons that periodically open into wide, flat valley bottoms. The steep-sided valley walls and wide, flat valley bottoms are the result of the advance and retreat of alpine glaciers during the Pleistocene epoch (Anderson *et al.,* 2006). The last glacial advance in the Rocky Mountain region, the Pinedale glaciation, extended down to ~2430 m and left a substantial terminal moraine that facilitated deposition of glacial outwash and formation of wide, flat valley segments that provide ideal habitat for beaver (Polvi and Wohl, 2012). The active and abandoned beaver meadows included in this study area are located above 2430 m, although Beaver and Cow Creeks did not have Pleistocene valley glaciers. In these unglaciated valleys, spatial variation in bedrock jointing causes longitudinal variation in valley geometry (Ehlen and Wohl, 2002; Wohl *et al.,* 2017), but the beaver meadow sites are narrower than those in the glaciated valleys.

The mean annual precipitation for the eastern half of RMNP is between 30 and 80 cm, with the majority of the precipitation falling as snow, leading to a snowmelt-dominated hydrograph for streams with headwaters in the park. These mountain streams seasonally flood during May or June at or exceeding bankfull stage in most years during the spring hydrograph snowmelt peak (Wohl *et al.,* 2004). Upland forests in the subalpine and montane zones in which our study meadows lie are dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) interspersed with aspen (*Populus tremuloides*) (Veblen and Donnegan, 2005). The valley bottoms contain a combination of meadow and riparian species such as grasses and sedges (*Carex* spp.), blue spruce (*Picea pungens*), river birch (*Betula fontinalis*), and willow (*Salix* spp.). The valley bottom species composition is highly related to beaver activity, with increased density of willow

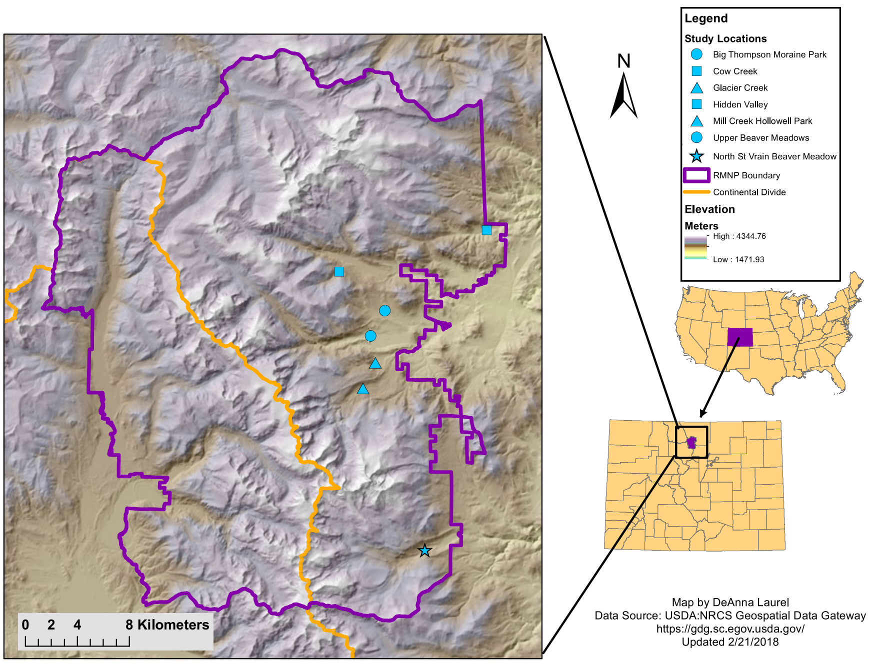

Figure 2. Location map of study meadows within Rocky Mountain National Park, Colorado, USA. The meadows are all east of the Continental Divide. [Colour figure can be viewed at wileyonlinelibrary.com]

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and wetland riparian species occurring in valley bottoms that display beaver influence in the channel and floodplain morphology (Polvi *et al.,* 2011).

Wolves were hunted to extinction in the RMNP during the 1920s and the numbers of elk and moose within the national park rose steadily during the twentieth century (Hess, 1993; Andrews, 2015). Although numerous active beaver colonies were present along several drainages of the park during the 1950s, by the start of the twenty-first century only a single spatially extensive, active beaver meadow remained. This site along North St Vrain Creek at the south-eastern boundary of the national park is our reference site for understanding the form and function of other beaver meadows within the national park. We compare measures of surface and subsurface geomorphic heterogeneity (form) and OC storage (function) among four categories of beaver meadows on the eastern side of the RMNP: active, partially active, recently abandoned, and long abandoned. Of our seven study sites on the eastern side of the national park, North St Vrain is the active meadow, with at least three active beaver colonies currently present at the site and beaver dams spread across the entire valley bottom. Hollowell Park (Mill Creek) and Glacier Creeks are the partially active meadows. Each has limited beaver activity present along the main channel and laterally across the valley bottom, but no beaver activity that is longitudinally and laterally continuous along the entire valley bottom. Glacier Creek has relict beaver structures throughout the meadow; Hollowell Park appears relatively unaffected by beaver presence outside of the limited area of current beaver activity. Cow Creek and Hidden Valley are the recently abandoned sites. Cow Creek had beavers present up until the 2013 flood that affected the Front Range of Colorado. This flood removed the dams along Cow Creek and beavers were still absent from this meadow during the data collection for this project in 2015 and 2016, although they have recently started to re-colonize the valley. Hidden Valley definitively had beavers as recently as the late 1990s, and likely more recently than that. Although the beavers have been gone from this meadow for at least 10 years, there remain many intact dams off the main channel, as well as secondary channels, beaver runs, and a seasonally inundated and infilling pond. Moraine Park (Big Thompson River) and Upper Beaver Meadows (Beaver Brook) are the long abandoned sites. Although beavers were present at these sites into the 1970s, no dams remain on the channels and the valley bottom is largely grassland with a single, incised channel. Although there are no visible remnants of the beaver morphology on the stream or the floodplain, buried dams and ponded sediments are present beneath the surface (Kramer *et al.,* 2012). Upper Beaver Meadows is included in the geomorphic heterogeneity analysis, but not the OC analysis. Table I summarizes meadow characteristics, including estimates of the time of abandonment.

Methods

Field methods and laboratory analyses

Fieldwork was conducted in the summers of 2015 and 2016. Geomorphic surveying involved walking transects perpendicular to the stream within each meadow, taking global positioning system (GPS) coordinates in the center of each geomorphic unit along a transect, and measuring the distance along the transect belonging to each geomorphic unit. Table II lists floodplain geomorphic units, which were distinguished by morphology, relative elevation above the main channel, and the vegetation community.

Sediment depth within geomorphic units was measured by pounding rebar into the ground until refusal by bedrock or cobble, or up to 1.5 m, the maximum length of the rebar probe. At each of four meadows (Hollowell Park, Hidden Valley, Cow Creek, Glacier Creek), 11 soil cores were collected for OC analyses based on the sample size necessary to accurately estimate floodplain soil OC storage in Front Range mountain streams (Sutfin and Wohl, 2017). Larger numbers of soil cores were collected at North St Vrain (23 cores) and Moraine Park (19 cores) because these sites represent end-members in the continuum of beaver activity between the study locations. Soil samples were collected along transects perpendicular to the main channel, with attention paid to distributing samples

Table II. Floodplain geomorphic units

Geomorphic unit	Description
Main channel	Primary active channel; perennial flow
Secondary channel	Secondary channels, with either perennial or ephemeral flow
Connected ponds	Ponds frequently connected by surface flow to the main channel
Disconnected ponds	Ponds without frequent connection to the main channel; secondary channels
Wetlands	Wetlands where the ground was saturated to the surface even during the driest part of the year
Seasonally inundated	Seasonally inundated higher floodplain surfaces that were saturated in the spring and early summer but dried later in the summer; common vegetation includes willows (*Salix* spp.), river birch (*Betula fontinalis*), grasses and sedges
Infrequently inundated	Higher and drier floodplain surface that is rarely inundated; vegetation includes xeric, upland plant species such as juniper (*Juniperus scopulorum*) and conifers (*Pinus* spp.)

Table I. Summary characteristics for the meadow study sites

Meadow	Drainage area (km^2)	Meadow area (km^2)	Beaver activity level	Length abandoned (years)
North St Vrain	89	0.42	Active	n.a.
Glacier Creek	36.7	0.02	Partially active	n.a.
Hollowell Park	14.7	0.19	Partially active	n.a.
Hidden Valley	9.3	0.04	Recently abandoned	< 20
Cow Creek	20.2	0.08	Recently abandoned	5
Moraine Park	110	2.57	Long abandoned	> 30
Upper Beaver Meadows	15	0.45	Long abandoned	> 30

Note: n.a., not available.

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among the different geomorphic units. At a sample location, ground vegetation was scraped clear to the surface of the mineral soil and samples were collected in 18 cm increments using a soil corer. Soils were sampled to the maximum corer depth (114 cm) or until the corer met with refusal. Refusal was primarily the result of encountering a gravel layer too coarse to sample, or encountering a larger clast or buried piece of wood. A small number of samples from ponds were limited in collection depth because the soil was too saturated to be extracted with the soil corer. Soil moisture samples from all sites were collected over a two-week period during base flow with no rainfall.

Samples were oven-dried for 24 hours at 105°C and soil moisture was calculated as the percent mass lost divided by the initial wet mass. The oven-dried mass of each sample, along with the volume of sediment collected in the soil corer, were used to calculate a bulk density for each sample. We assigned a texture class to the mineral soil in each sample following the USDA Natural Resources Conservation Service guidelines for hand texturing (National Resources Conservation Service [NRCS], 1996).

Organic carbon concentration of the soil samples was measured at the Soil, Water, and Plant testing laboratory at Colorado State University. Samples were sieved to separate the < 2 mm fraction, then the total carbon concentration (%) of the < 2 mm fraction was measured using a LECO TruSpec CN furnace (Nelson and Sommers, 1982). Inorganic carbon was measured by treating the sample with 0.4 hydrochloric acid (HCl) and measuring the carbon dioxide (CO_2) loss gravimetrically (NRCS, 1996). Subtracting the inorganic carbon from the total carbon concentration provided the OC concentration (%).

These field and laboratory data were used to quantify response variables that we related to the control variable level of beaver activity. Response variables evaluated here are surface geomorphic heterogeneity, subsurface geomorphic heterogeneity (sediment depth, soil moisture, percent clay content, OC concentration), and total soil OC stock of each meadow.

Statistical methods

Surface geomorphic heterogeneity was quantified using several different metrics. First, we calculated the number of distinct geomorphic units per kilometer of valley width from the floodplain transect surveys, as a measure of spatial heterogeneity derived from Graf (2006). These values were compared across the seven study meadows using analysis of variance (ANOVA), and compared to each other with pairwise comparisons with a Tukey adjustment for multiple comparisons. Analyses were run in the statistical software R. We also characterized the meadow surface heterogeneity utilizing diversity metrics commonly used by ecologists that include how many different types of features (here, geomorphic units) are present in a beaver meadow, which is richness, and how evenly these features are distributed within the meadow (i.e. how many of each feature are present), which is evenness. We used the Shannon Diversity Index and Shannon Equitability (Shannon, 1948), and the Simpson's Index of Diversity (Simpson, 1949).

$$\text{Shannon Diversity Index} \quad H = -\sum_{i=1}^{S} p_i(\ln(p_i)) \qquad (1)$$

$$\text{Shannon Equitability} \quad E_H = H/\ln S \qquad (2)$$

$$\text{Simpson's Diversity Index} \quad D = 1 - \left(\frac{\sum n(n-1)}{N(N-1)}\right) \qquad (3)$$

where n is number of individuals in each species (e.g. number of ponds within the geomorphic unit pond), N is the total number of individuals (i.e. total number of geomorphic units measured), p_i is the proportion n/N, and S is the number of species (i.e. number of types of geomorphic units), or the richness. Both the Shannon Diversity Index and the Simpson's Diversity Index combine the richness and the evenness of species into one value in order to make comparisons between sites. The Shannon Diversity Index places greater weight on the richness of features, whereas the Simpson Diversity Index prioritizes relative abundance of the different features in the calculation. Higher values of the Shannon and Simpson's Diversity metrics indicate greater diversity, or in this case, greater geomorphic heterogeneity. The Shannon Equitability index is simply H divided by H_{max} (here, ln S), and assumes a value between zero and one, with one being complete evenness. Finally, we graphically displayed the proportion of surveyed meadow that falls into each geomorphic unit category with pie charts in order to visually compare the heterogeneity in these environments.

We characterized subsurface geomorphic heterogeneity for six of the meadows (Upper Beaver Meadows not included) based on four metrics: soil moisture, soil depth, percent clay content (derived from hand texturing), and OC concentration (%OC). We assessed soil moisture and percent clay content because of their potential influence on plant growth and soil OC content. We assessed soil depth and carbon concentration because of their influence on carbon stock. Comparisons of soil moisture, soil depth, %clay, %OC, and OC stock (in Mg OC/ha) were made across geomorphic units, across study meadows, and across levels of beaver activity using the nonparametric Kruskal–Wallis test with a Bonferroni adjustment for multiple comparisons to assess whether beaver activity and the resulting geomorphic heterogeneity led to significantly different soil moisture, soil depth, %clay, or OC content (% or stock).

A linear regression model was fit to the %OC and stock OC data to investigate correlations between predictor variables and OC content. Initially, a linear mixed effects model was chosen to account for potential random effects associated with the sampling design (along transects), but a comparison of models found that including a random effect was not necessary, so a simple multiple linear regression model was used instead. The predictor variables investigated included geomorphic unit, depth of sample (the middle value of each sample for %OC and the total core depth for OC stock), soil moisture, percent clay content, drainage area, and geomorphic heterogeneity calculated as the number of distinct geomorphic units per kilometer of valley width. Organic carbon content was modeled as the %OC in each sample, and as the OC stock aggregated over each core. The residuals of each model were checked to verify that the model assumptions were being met, including verifying the homoscedasticity of variance. In order to meet the model assumptions, the response variables were transformed: %OC was square root transformed and OC stock was natural log transformed. The significance of each predictor variable in the model was tested at alpha = 0.05 to determine which predictor variables have explanatory power, and hence influence the variability in OC concentration or stock. The linear regression models were run in R, utilizing the lm() function.

Results

Surface geomorphic heterogeneity

We characterized surface heterogeneity using the seven geomorphic units described in the methods (Table II). Simple visual comparison of the proportion of surface area in each

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geomorphic unit indicates that the long abandoned meadows (Upper Beaver Meadows and Moraine Park) have lower diversity of geomorphic units and less surface water than the active meadow (North St Vrain) (Figure 3). The partially active meadows and recently abandoned meadows lie along a continuum between these end-members. Using the geomorphic heterogeneity metric derived from Graf (2006), the long abandoned meadow at Moraine Park differs significantly from all of the other sites (Figure 4). (The long abandoned meadow Upper Beaver Meadow does not differ significantly from recently abandoned sites.) All three ecological metrics of diversity, applied here to surface geomorphic heterogeneity, indicate the highest heterogeneity in the active meadows. Heterogeneity decreases to the lowest level in the abandoned meadows with the exception of Hidden Valley, which has heterogeneity comparable to the active meadows (Table III). Simpson's and Shannon's Diversity indices are notably lower for the abandoned beaver meadows. Shannon's Equitability indicates greater evenness between geomorphic units in the active meadows than the abandoned meadows. Evenness also decreases with time since meadow abandonment (Table III).

These analyses support H1. Most indicators suggest that the geomorphic heterogeneity of the active beaver meadow mostly does not differ significantly from partially active and recently abandoned meadows (active North St Vrain does differ significantly from partially active Hollowell). This suggests a non-linear decrease in surface geomorphic heterogeneity with time since beaver abandonment.

Subsurface geomorphic heterogeneity

We examined soil moisture at the level of individual samples (vertical increments within a core) and the entire core. Soil moisture differs significantly at all scales considered. We focus on results at the core level because the trends and significance were the same for the sample level data. Mean core soil moisture differs significantly in the active meadow (North St Vrain) and the long abandoned meadow (Moraine Park), but other meadows are gradational between these end-members (Figure 5, see also Supporting Information Figure S1). Mean core soil moisture shows few significant differences among geomorphic units (Figure S2).

Soil core depth does not differ significantly among geomorphic units (Figure S3), but does differ significantly among meadows (Figure S4). Soil core depth of partially active and recently abandoned meadows differs significantly from that of active and long abandoned meadows, which are similar to one another (Figure 5). Clay content does not differ significantly among geomorphic units, with respect to level of beaver activity, or among sites.

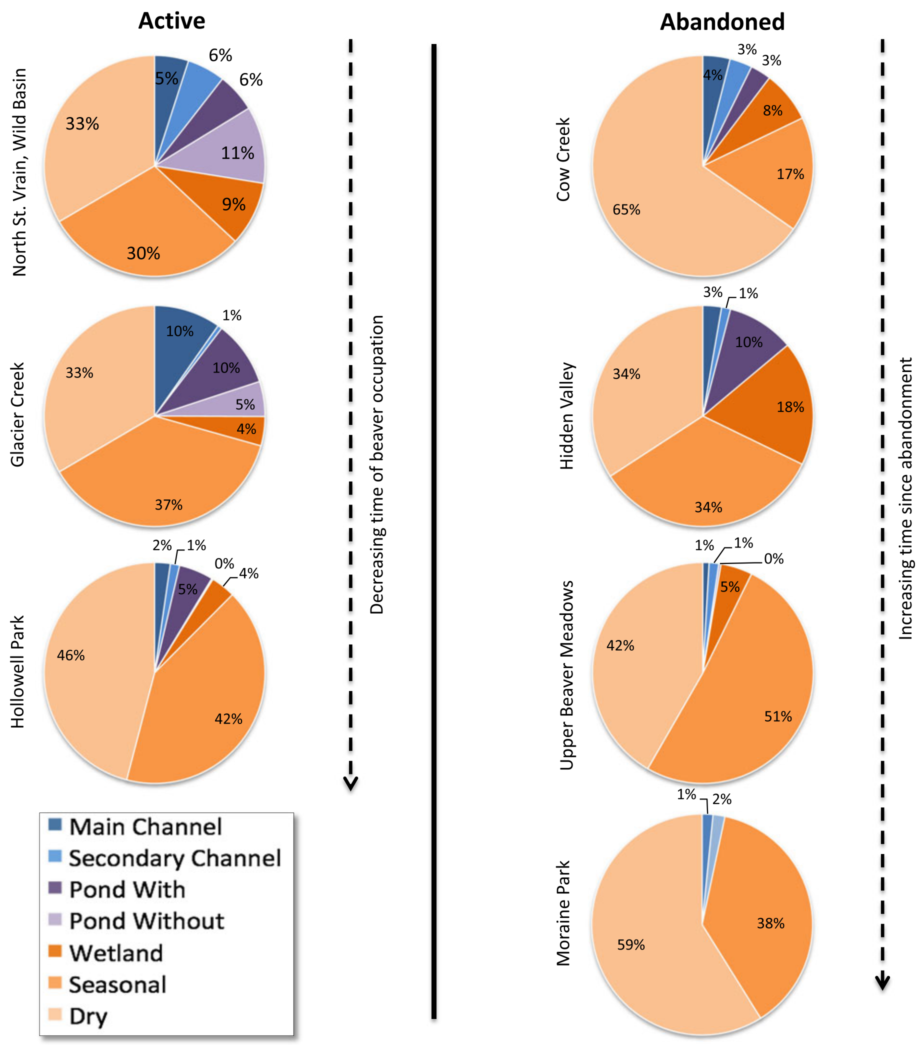

Figure 3. Visual representation of surface spatial heterogeneity in relation to level of beaver activity within a meadow. Total percent surface water is the sum of the percent channel and pond features for each meadow. [Colour figure can be viewed at wileyonlinelibrary.com]

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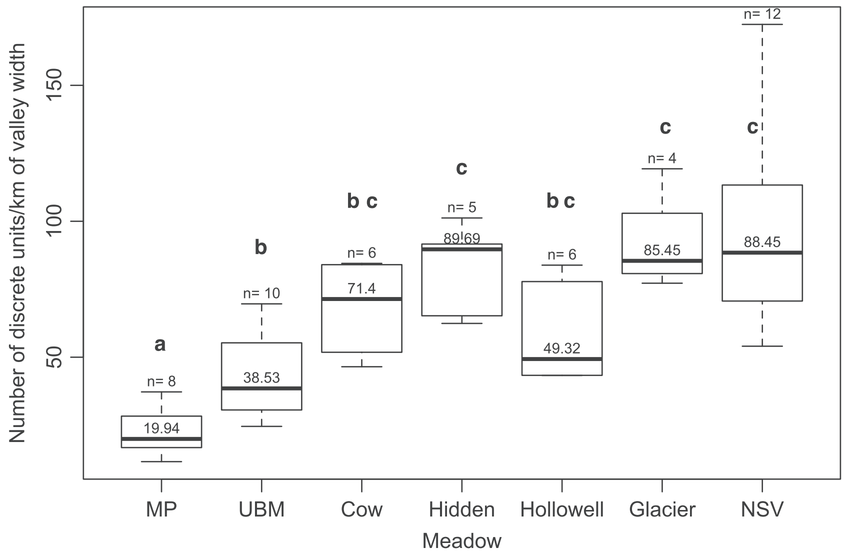

Figure 4. Surface spatial heterogeneity as indicated by the metric derived from Graf (2006) in relation to individual beaver meadows. Letters indicate significant differences between median values. Median value and sample size indicated for each meadow. In total, 51 transects were sampled. MP, Moraine Park; UBM, Upper Beaver Meadows; Cow, Creek; Hidden Meadow, Hidden Valley; Hollowell, Hollowell Park; Glacier, Glacier Creek; NSV, North St Vrain.

Table III. Metrics of surface geomorphic heterogeneity

Meadow	Average number of units per kilometer of valley width	Simpson's Index of Diversity (D)	Shannon Diversity Index	Shannon's Equitability (E_H)
North St Vrain	95.268	0.779	1.639	0.915
Glacier Creek	91.856	0.742	1.495	0.835
Hollowell Park	57.821	0.713	1.448	0.808
Hidden Valley	82.037	0.765	1.535	0.857
Cow Creek	68.275	0.670	1.284	0.717
Upper Beaver Meadows	42.769	0.547	0.991	0.715
Moraine Park	22.359	0.475	0.816	0.589

Organic carbon concentration does not differ significantly between geomorphic units (Figure S5) but does differ significantly among meadows (Figure S6). Most importantly in the context of our hypotheses, OC concentration does not differ significantly between meadow categories (Figure 5).

Thus, with respect to subsurface geomorphic heterogeneity, only soil moisture appears to decrease non-linearly with time since beaver abandonment (H1).

We also modeled OC concentration at the level of individual samples (Table IV). Using a multiple linear regression model, geomorphic unit, soil moisture, clay content, depth, drainage area, and geomorphic surface heterogeneity are all significant predictor variables (Table IV).

Total floodplain soil organic carbon stock

Organic carbon stock does not differ significantly among geomorphic units (Figure S7). Organic carbon stock does differ significantly among meadows, although not in a manner that clearly relates to level of beaver activity (Figure S8). Similarly, the differences in OC stock in relation to meadow category do not show a linear or non-linear decrease with time (Figure 6) and thus do not support our hypothesis (H2).

We also modeled OC stock at the level of individual cores. Using a multiple linear regression model, geomorphic unit, clay content, soil moisture, the surface heterogeneity metric, and total depth of the core are all significant predictor variables (Table IV), but stepwise model progression indicates that clay content, total depth, and the surface geomorphic heterogeneity metric are the most important predictors of OC stock.

Finally, we estimated OC stock for each meadow. These estimations are a first-order approximation because we calculated volume of the upper meadow soil (≤ 1.5 m depth, depending on the average maximum depth reached within each meadow) and used the median soil bulk density and median OC concentration for each meadow to calculate stock. The results (Table V) clearly indicate that level and timing of beaver activity are not the primary control on OC stock within a meadow and that OC stock does not differ between active and long abandoned meadows.

Discussion and Conclusions

Measures of surface geomorphic heterogeneity support the first hypothesis, which is that geomorphic heterogeneity decreases non-linearly with time since beaver abandonment. Partially active and recently abandoned meadows do not differ significantly from the active meadow, whereas the long abandoned meadows are significantly different. Among measures of subsurface geomorphic heterogeneity, only soil moisture varies in a manner that supports the first hypothesis. Soil depth appears to be controlled by other factors; clay content is likely similar

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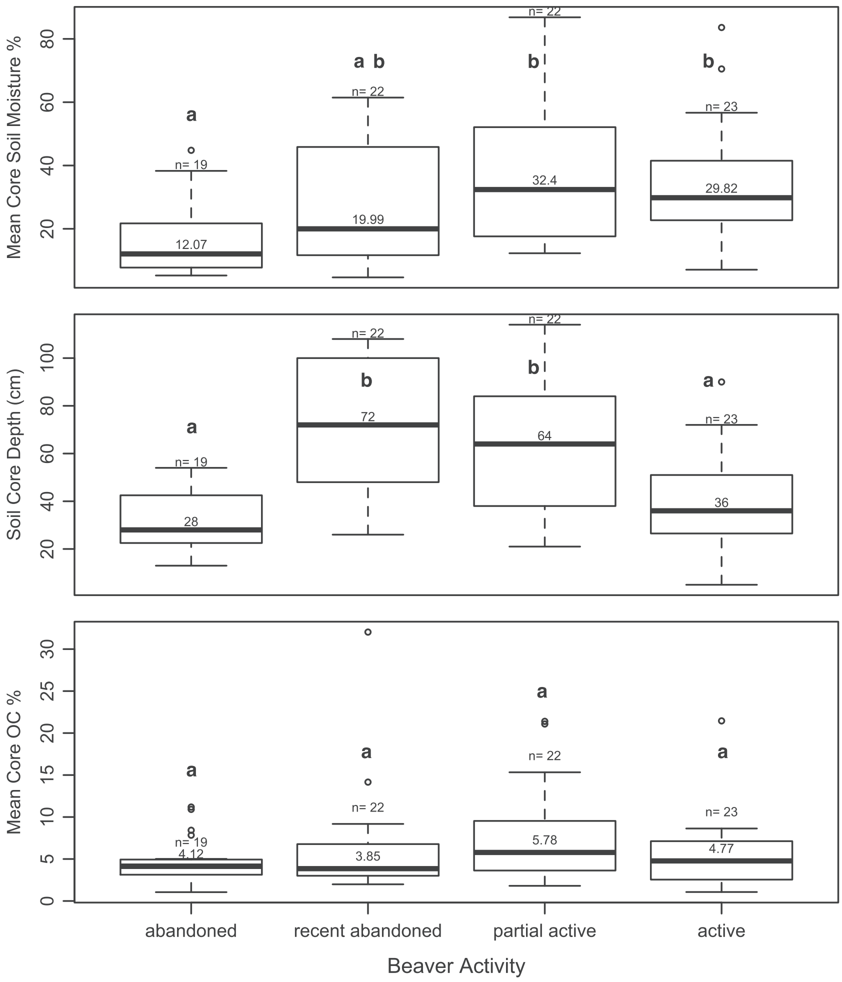

Figure 5. Mean core soil moisture percent, soil core depth, and mean organic carbon concentration by core, in relation to beaver meadow categories. Letters indicate significance differences between mean values (comparisons made using non-parametric Kruskal–Wallis test with Bonferroni adjustment for multiple comparisons at the 0.05 significance level). Median value and sample size indicated for each meadow category.

Table IV. Summary of multiple linear regression model results for modeling organic carbon (OC) (%) at the sample level and OC stock (Mg C/ha) at the soil core level

	OC (%)	OC stock (Mg C/ha)
Geomorphic unit	**<0.0001 (6.97)**[c]	**0.046 (2.50)**
Soil moisture[a] (%)	**<0.0001 (112.6) [0.0319]**[d]	0.671 (0.182) [−0.0026]
Clay content[a] (%)	**<0.0001 (114.6) [0.0201]**	**<0.001 (16.4) [0.0166]**
Depth[b] (cm)	**0.0015 (10.3) [−0.0109]**	**<0.0001 (121.0) [0.0215]**
Drainage area (km^2)	**0.0056 (7.80) [−0.00531]**	0.363 (0.839) [−0.00253]
Geomorphic surface heterogeneity	**<0.0001 (16.83) [−0.0099]**	**0.011 (6.71) [−0.00668]**

Note: Values shown in bold typeface are significant at alpha = 0.05.
[a]Averaged over the core for the OC stock model.
[b]For the OC (%) model, the depth is the middle depth (in centimeters) of the sample increment; for OC stock, it is the total depth of the soil core (in centimeters).
[c]*p* Value (*F* statistic).
[d][coefficient β; effect of a unit increase of the predictor on the response].

between sites because of the consistent geology and very limited supply of clay in the study area; and soil OC stock seems to be strongly influenced by soil depth.

The results generally do not support the second hypothesis, which is that floodplain soil OC stock does not decline linearly with time following beaver abandonment of a river corridor. Floodplain soil OC stock does not decline linearly with time (Figure 6), but the primary controls appear to be factors other than beaver activity. Soil depth appears to be particularly influential. The meadows with the greatest soil depths are those in the partially active and recently abandoned categories, and these categories also have the greatest carbon stock.

Geologic factors, rather than beaver activities, may exert the primary control on variations in soil depth among beaver meadows. The Hidden Valley meadow may have the greatest soil depth (Figure S4) and core-level OC stock (Figure S8)

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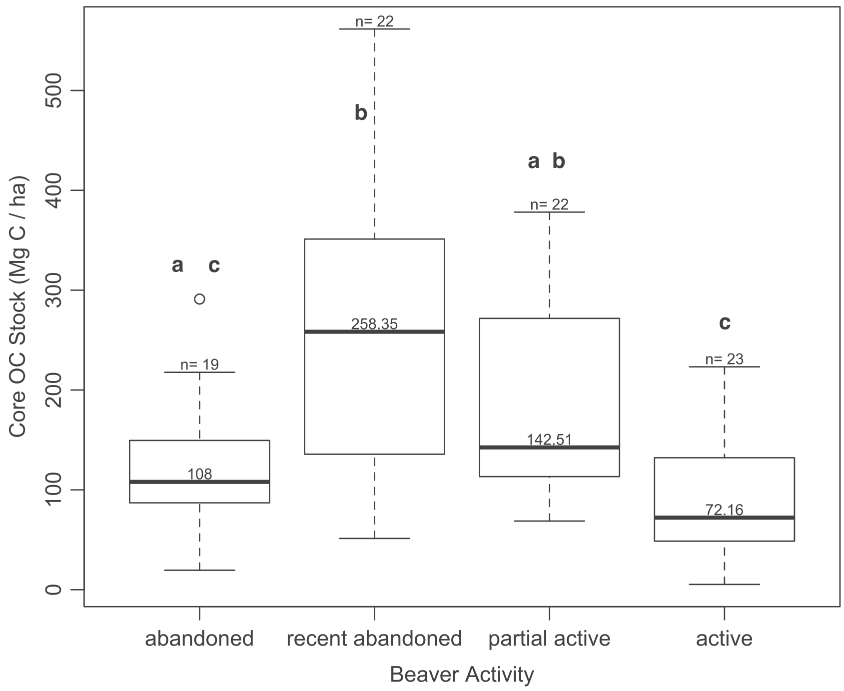

Figure 6. Mean organic carbon (OC) stock, by core, in relation to beaver meadow category. Letters indicate significance differences between mean values (comparisons made using non-parametric Kruskal–Wallis test with Bonferroni adjustment for multiple comparisons at the 0.05 significance level). Median value and sample size indicated for each meadow category.

Table V. Estimated values of total organic carbon (OC) stock in the upper portion (≤ 1.5 m depth) of each of the studied meadows, which are listed from active in the first row to long abandoned in the last row

Meadow	Total OC (Mg C)	OC stock (Mg C/ha)
North St Vrain	13166	313
Glacier Creek	599	300
Hollowell Park	10175	536
Hidden Valley	2059	515
Cow Creek	15701	349
Upper Beaver Meadows	25272[a]	562[a]
Moraine Park	142445	554

[a]Values based on data in Wohl (2013) for this site.

because it is the only site studied here that has a base level above the Pleistocene terminal moraine. Hidden Valley Creek is tributary to the Fall River, which cuts through the terminal moraine. The small drainage area and stable, higher base level may facilitate sediment storage within the Hidden Valley beaver meadow. Conversely, the active North St Vrain site and the long abandoned Moraine Park site may have the shallowest soil depths because these sites have the largest upstream drainage area, which may equate to greater transport capacity and lateral channel mobility in the beaver meadows. An important caveat to these interpretations is that we are only considering the upper 1.5 m of alluvium in each site. The large drainage area and multiple episodes of Pleistocene glaciation (Madole, 2012) in the Moraine Park drainage suggest that buried soils may be present beneath the cobble and boulder layer that limited our coring, but this deeper material is not considered in our analyses.

Soil OC stock reflects the balance among (i) carbon inputs from autochthonous sources (riparian vegetation litterfall and stems cut by beavers) and allochthonous sources (overbank deposition of fluvially transported organic matter), (ii) carbon outputs via fluvial erosion of floodplain soil and organic matter, and (iii) carbon storage, which in turn reflects soil depth as well as sorption capacity and respiration rate (Figure 7). Sorption capacity and respiration rate reflect factors such as moisture content, temperature, and mineralogy (Scott and Wohl, in review). Although moisture content can reflect channel–floodplain connectivity as this influences riparian water table, moisture content can also reflect soil texture and groundwater inputs. The presence in the RMNP of fens and wet meadows not associated with valley bottoms indicates that the highly fractured crystalline bedrock of the region can support seeps and springs that create carbon-rich environments apart from beaver activity (Clow *et al.,* 2003; Liu *et al.,* 2004), and groundwater inputs to valley bottoms likely also influence carbon stock along some portions of the river network.

With respect to carbon inputs, recent work on other floodplains in the Rocky Mountains and elsewhere suggests that autochthonous inputs dominate (Scott and Wohl, in review; Lininger *et al.,* 2018). The lack of buried, high OC concentrations at depth in the soil cores from the beaver meadows suggests that autochthonous, rather than allochthonous, inputs also dominate these floodplains. While beavers are present in a meadow, their activities maintain high levels of autochthonous inputs via dense aquatic and riparian vegetation across floodplains and high levels of carbon storage via high riparian water tables. By creating an anastomosing channel planform, however, beavers may also increase carbon outputs via accelerated bank erosion and limited carbon deposition and storage in secondary channels except where beaver ponds are present on these channels (Sutfin, 2016). When beaver activity ceases as a result of competition from ungulates, the change in riparian vegetation toward bunchgrasses and small shrubs more characteristic of a semi-arid steppe presumably reduces autochthonous carbon inputs (Buell and Markewich, 2004) and the incision of the main channel lowers the riparian water table and reduces carbon storage as floodplain soils dry (Trumbore and Czimczik, 2008), but the reversion to a single channel may reduce carbon

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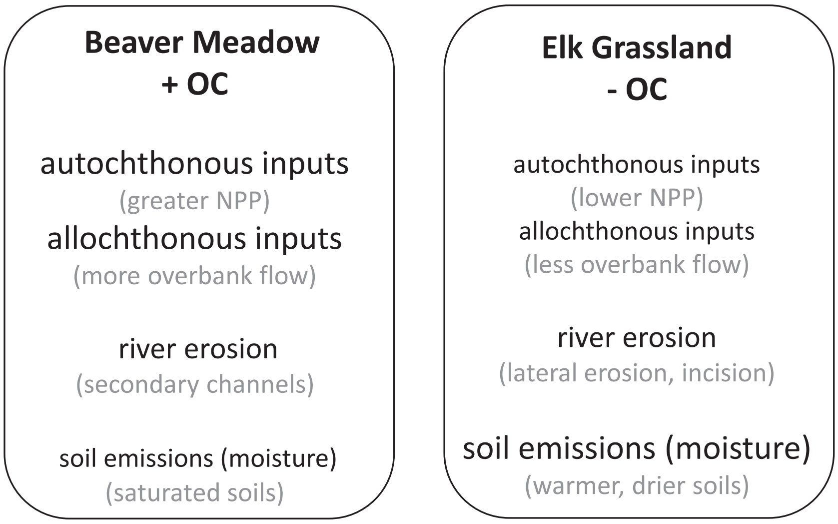

Figure 7. Schematic illustration of differences in the relative importance of diverse inputs, outputs, and controls on organic carbon (OC) storage in beaver meadows versus elk grasslands (NPP refers to net primary productivity). Relative size of black text within each box indicates relative importance of the process between the two scenarios (e.g. soil emissions of OC are likely greater from elk grasslands).

outputs via fluvial erosion. If the single channel remains relatively stable, the abandoned beaver meadow may remain capable of storing substantial OC stocks. This is particularly important in a management context because active or abandoned beaver meadows account for disproportionately large amounts of the OC stored along valley bottoms in river networks (Wohl *et al.,* 2012), so maintaining even abandoned beaver meadows in a stable (rather than actively eroding) state can foster carbon storage.

Fundamentally, soil OC stock within a beaver meadow reflects soil depth, which is strongly influenced by geological factors of glacial history, bedrock geology, and drainage area. Beavers build on this geological template to create a heterogeneous environment that fosters high levels of soil moisture, finer textured floodplain soils, and higher inputs of autochthonous OC, all of which enhance the OC concentration and thus the overall stock. When beavers abandon a meadow, the persistence of stored OC is governed by rates and magnitudes of change in sediment storage within the meadow, as well as OC concentration within the floodplain soil.

Returning to the initial conceptual model (Figure 1), we do not see evidence for an abrupt threshold such that a beaver meadow changes significantly as soon as beavers abandon a site. Instead, several years are required before the effects of beaver ecosystem engineering are lost as dams disappear, secondary channels become inactive, and ponds are filled. In our study region on the eastern side of the Colorado Front Range, these changes seem to require *c.* 30 years to create significant differences in geomorphic heterogeneity and associated function. Storage of OC in floodplain soils, however, may persist for much longer periods if the abandoned meadow remains stable (rather than subject to extensive lateral channel migration and fluvial erosion).

Our ability to quantify rates of change with beaver abandonment is limited by the fact that beaver have not abruptly left any of the sites that we studied. Instead, individual animals and colonies of beavers come and go through time. Since the fieldwork described here, for example, beavers have recolonized the downstream portion of the Cow Creek site. At the North St Vrain meadow, the location of individual dams and the status (filled or drained) of individual ponds changes each year. We used categories of beaver activity because of the difficulty in quantifying the number of beaver and active colonies within a meadow. With this caveat, however, our results indicate that the effect of beaver ecosystem engineering can persist for at least several years following a significant decline in beaver activity or abandonment of a site. This is important in the context of the increasing use of beaver reintroduction as part of river restoration (e.g. Burchsted *et al.,* 2010; Pollock *et al.,* 2014). Methylation of mercury, for example, occurs at much lower rates where beavers reoccupy historic beaver meadows than where the animals create new wetlands (Levanoni *et al.,* 2015). This highlights the importance of either actively reintroducing beaver to abandoned sites or enhancing conditions at abandoned sites in a manner that facilitates recolonization by beaver.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Median core soil moisture differs significantly in the active meadow (NSV) and the long abandoned meadow (MP), but other meadows are gradational between these end-members. Letters indicate significant differences. Median values and sample size are listed for each meadow.

Figure S2. Core soil moisture by geomorphic unit. Letters indicate significant differences. Median values and sample size are listed for each floodplain geomorphic unit.

Figure S3. Soil core depth in relation to geomorphic unit. No significant differences in median soil core depth among geomorphic units. Median values and sample size are listed for each floodplain geomorphic unit.

Figure S4. Soil core depth by meadow. Letters indicate significant differences. Median values and sample size are listed for each meadow.

Figure S5. Core organic carbon concentration in relation to geomorphic unit. No significant differences in median core OC concentration among geomorphic units. Median values and sample size are listed for each floodplain geomorphic unit.

Figure S6. Core organic carbon concentration in relation to meadow. Letters indicate significant differences. Median values and sample size are listed for each meadow.

Figure S7. Core organic carbon stock in relation to geomorphic unit. No significant differences in median core OC stock among geomorphic units. Median values and sample size are listed for each floodplain geomorphic unit.

Figure S8. Core organic carbon stock in relation to meadow. Letters indicate significant differences. Median value and sample size are listed for each meadow.

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